From ecosystems to people: Examining the variability in the provision of ecosystem services by eelgrass meadows in Atlantic Canada

by

Tanya S. Prystay

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Land Acknowledgement

We respectfully acknowledge the territory in which we gather as the ancestral homelands of the Beothuk, and the island of Newfoundland as the ancestral homelands of the Mi’kmaq and Beothuk. We would also like to recognize the Inuit of Nunatsiavut and NunatuKavut and the Innu of Nitassinan, and their ancestors, as the original people of Labrador. We strive for respectful relationships with all the peoples of this province as we search for collective healing and true reconciliation and honour this beautiful land together.

Abstract

Seagrass meadows provide functions that support other species and ecosystem services that directly and indirectly benefit human wellbeing. However, growing in estuarine environments, seagrass meadows are exposed to interacting pressures from terrestrial and marine systems, resulting in their degradation worldwide. Efforts to conserve these social-ecological systems have met challenges, including insufficient maps to assess seagrass status and value, a limited understanding of seagrass meadow ecosystem traits underpinning the provision of ecosystem services, and a lack of public awareness necessary to support management decisions. This thesis presents multidisciplinary studies of eelgrass (*Zostera marina*) meadows in Placentia Bay, Newfoundland and Labrador, Canada, that contribute toward addressing these challenges. In the first study, I evaluated the reproducibility of using remotely piloted aircraft systems (RPAS) to collect seasonal maps of submerged eelgrass meadows in a temperate environment. I show that higher altitude surveys are beneficial when surveying in rapidly changing environments; however, RPAS surveys using three-colour band imagery alone may be insufficient to discriminate seasonal changes. In the second and third studies, I identified meadow structural and environmental traits underpinning eelgrass service as fish habitat and function as a coastal filter. In the second study, I show that shallower and more saline eelgrass meadows enhance diversity in fish life history traits. In the third study, I show that carbon and nitrogen content in the surface sediment was negatively related to sediment density, where isotopic ratios indicated that the carbon was predominantly derived from marine allochthonous (non-eelgrass) sources. Lastly, in the fourth study, using an online survey, I show strong awareness of eelgrass by Canadian coastal Atlantic community members, and support for conservation efforts. Participants identified fish habitat, coastal protection, and water quality maintenance as the three most important ecosystem services provided by eelgrass in Atlantic Canada. Together, the components of this thesis characterise three Newfoundland and Labrador eelgrass meadows, the services they provide, and synthesises the perception of eelgrass by Canadian coastal Atlantic community members. These findings are relevant to local management decision-making and eelgrass monitoring, while also contributing to the growing global characterization of the variability in eelgrass meadow function driving ecosystem services.

General Summary

Seagrasses are marine plants that create meadows along the coast, where freshwater meets the ocean. Seagrass meadows occur globally and have traits that benefit other species and humans. For instance, by extending vertically into the water column, seagrass trap nutrients. In doing so, seagrass meadows provide nutrient rich and structured habitats for fish and invertebrates. These benefits, termed ecosystem services, vary according to seagrass meadow structure and with the surrounding environment. Despite their importance, seagrass meadows are exposed to threats from terrestrial and marine systems, resulting in loss of seagrass worldwide. Efforts to conserve seagrass meadows have been met with challenges, including insufficient maps of seagrass meadow locations and status across geographic regions and limited understanding of meadows traits that support their benefits to other species and humans. This thesis studied eelgrass, a species of seagrass, in Placentia Bay, Newfoundland and Labrador, Canada, to contribute to the collective understanding of eelgrass meadow traits and resulting benefits. The first study in this thesis focuses on collecting seasonal maps of eelgrass meadows using aerial drones. The second and third studies in this thesis identified meadow structural (e.g., blade length, meadow patchiness) and environmental (e.g., water temperature, salinity) traits underpinning eelgrass benefits as a fish habitat and ability to trap nutrients. These studies showed that eelgrass meadows support various fish species and retain nutrients in the coastal zone, but that the level at which each meadows provides these benefits is meadow dependent (i.e., support different fish species, trap different amounts of nutrients). Lastly, through an online survey, the fourth study revealed a strong awareness of eelgrass by

Canadian coastal Atlantic community members that participated in the survey. Public awareness is necessary for informed decision making. Thus, this study exposed an opportunity to use this public support to expand conservation efforts. Together, this multidisciplinary thesis characterises three Newfoundland and Labrador eelgrass meadows and the benefits they provide and synthesises the public perception of eelgrass by Canadian Atlantic community members. These findings are relevant to local management decision-making and contribute to global understanding of eelgrass meadow traits that yield benefits to other species and people.

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I am grateful to my supervisor, Dr. Arnault Le Bris, who encouraged me to take on a multidisciplinary thesis, which has led me to broaden my research scope and interests. I am also grateful to my thesis committee, Dr. Rachel Sipler, Dr. Robert Gregory, and Dr. Brett Favaro, for their exceptional guidance and support as I explored these new disciplines throughout my Ph.D. journey. Their mentorship, patience, and thought-provoking discussions enriched my experience as a graduate student. Collectively, Arnault and my thesis committee members, positively shaped my development as a scientist and a person, and I am tremendously thankful to have had the opportunity to work with each of them.

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Co-authorship statement

This manuscript-style thesis is comprised of four co-authored manuscripts. Each manuscript is currently at various stages of the peer-reviewed publication process or is currently in preparation for submission into a peer-reviewed journal. Given each of these chapters is designed to submit as a stand-alone peer-reviewed research article, some definitions (e.g., ecosystem services) and study site descriptions are repeated in more than one chapter. I collected all the data used in this thesis with the help of my supervisor, technicians, and research assistants. All datasets will be made available through online data repositories after publication.

The research in each manuscript comprising this thesis was a collaborative effort given the multidisciplinary nature of the studies I undertook. All co-authors contributed critical input to the manuscript and have provided consent (or will have provided consent) prior to the publication of the research. Co-author contributions to each chapter are outlined below. This list only includes collaborators that contributed directly to the preparation of the manuscripts in this thesis. Additional collaborators were also essential to the realization of the research and are recognized in the Acknowledgements of this thesis.

Chapter 2

Prystay TS, Adams G, Favaro B, Gregory RS, Le Bris A. 2023. The reproducibility of remotely piloted aircraft systems to monitor seasonal variation in submerged seagrass habitats. FACETS. 8:1-22. Doi.org/10.1139/facets-2022-0149

Prystay, Le Bris, Favaro, and Gregory conceptualized the ideas and designed the methodology. Prystay led the data collection with help from Adams. Prystay analysed the data and led the writing of the manuscript. All authors contributed edits to the draft. Prystay presented two workshops to Fisheries and Oceans Canada covering skills and methods used in this manuscript.

Chapter 3

Prystay TS, Gregory RS, Le Bris A. Characterizing eelgrass meadow traits that promote fish taxonomic and life history diversity. *In prep* for Marine Ecology Progress Series.

Prystay, Le Bris, and Gregory developed the idea for this paper. Prystay and Le Bris designed the study, and Prystay led the data collection and analysis. Writing of the manuscript was also led by Prystay with assistance from Le Bris and Gregory.

Chapter 4

Prystay TS, Sipler RE, Foroutani MB, Le Bris, A. The role of seagrass meadows in the coastal filter in a temperate boreal system. *Submitted* to Journal of Geophysical Research: Biogeosciences.

Prystay, Sipler, and Le Bris conceptualized the ideas for this manuscript. Prystay led the data collection with laboratory assistance from Foroutani and Sipler. Prystay also led the writing of the manuscript with feedback from Sipler and LeBris. Using research from this chapter, Prystay also co-authored the seagrass section in the WWF Canada Coastal Blue Carbon in Canada: State of Knowledge report (Kelly et al. 2023).

Chapter 5

Prystay TS, Neis B, Sullivan SM, Le Bris A. 2023. Coastal community perceptions of eelgrass in Atlantic Canada: Considerations for management. *Oceans and Coastal Management*. 239(15). doi: https://doi.org/10.1016/j.ocecoaman.2023.106600

Prystay and Le Bris conceived the ideas for this manuscript. Prystay designed the methodology with assistance from Le Bris and Neis, and distributed the survey with help from Le Bris (and others). The literature review was conducted by Prystay and Sullivan, and Prystay analyzed the data and led the writing of the manuscript with feedback from Neis and Le Bris. The development of this research was broadcasted via an interview with Prystay on *CBC Radio's Fisheries Broadcast* in 2020.

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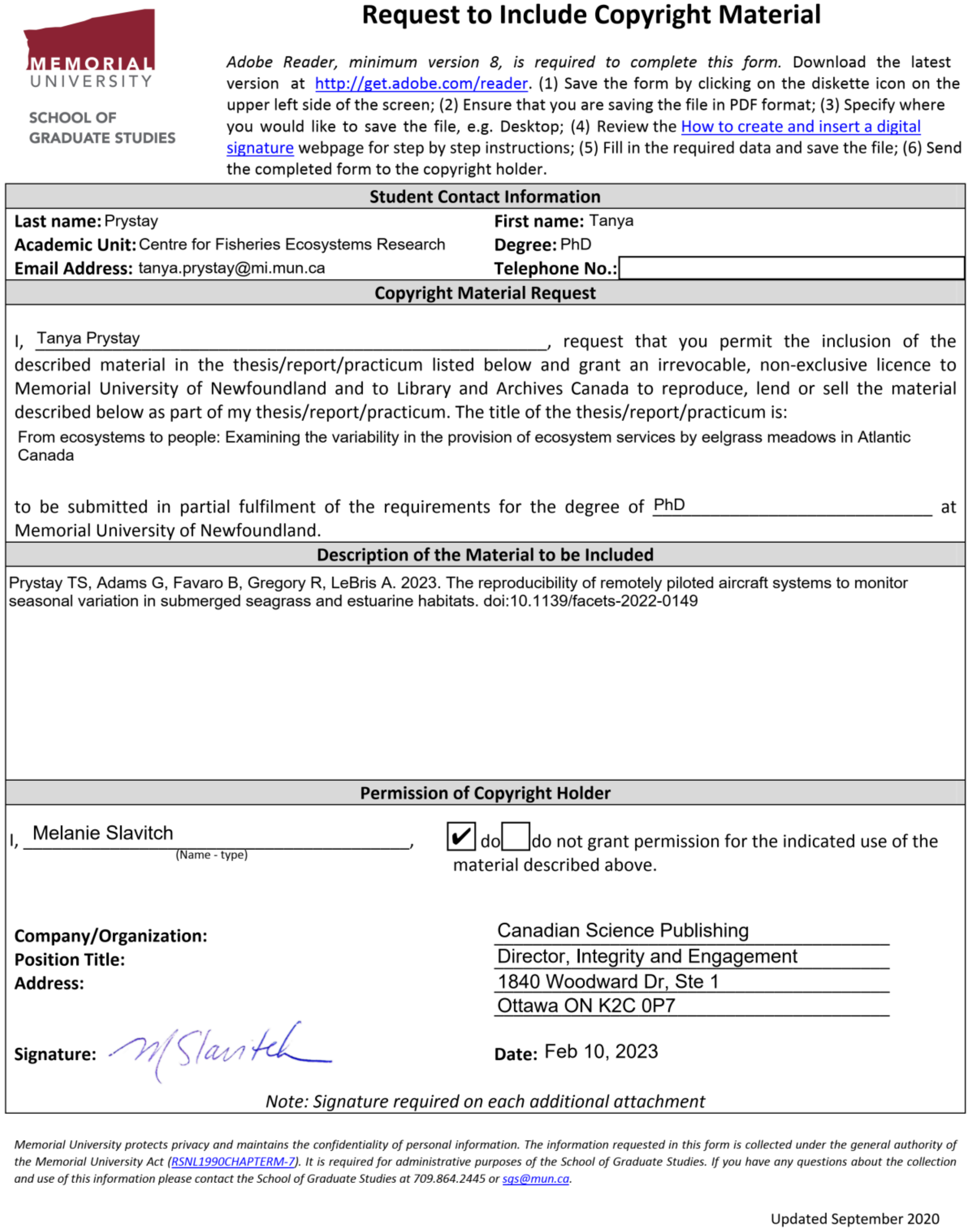

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Student Contact Information

Last name: Prystay
First name: Tanya
Academic Unit: Centre for Fisheries Ecosystems Research
Degree: PhD
Email Address: tanya.prystay@mi.mun.ca
Telephone No.:

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List of Abbreviations and Symbols

AIC – Akaike information criterion

BL – Baie de l’eau

$\delta^{13}C_{org}$ – carbon isotopic signature

°C – degree Celsius

C_{org} – organic carbon

$\%C_{org}$ – organic carbon content

C:N – ratio between organic carbon and nitrogen content

CO_2 – carbon dioxide

DO – dissolved oxygen

GLMM – generalized linear mixed model

LHT – life history trait

N – nitrogen

$\delta^{15}N$ – nitrogen isotopic signature

%N – nitrogen content

NH – North Harbour

NTU – nephelometric turbidity unit

PIC – particulate inorganic carbon

psu – practical salinity unit

RGB – red, green, blue

RPAS – remotely piloted aircraft system

SC – Swift Current

TL – total length

Chapter 1: General Introduction

1.1 Seagrass overview and status

“*We are all together in this, we are all together in this single living ecosystem called earth. As we learn how we fit into the greater scheme of things and begin to understand how the system works, we can plan ahead, we can use the resources responsibly...*”
– Dr. Sylvia Earle

Seagrasses are marine flowering plants that occur along the coastlines of every continent except Antarctica (Hemminga and Duarte 2000a; Green and Short 2003; Orth et al. 2006) (Figure 1.1). Growing in estuarine environments, the intersection between “two worlds” – namely freshwater and marine systems – seagrass meadows provide ecosystem functions (i.e., subset of ecological processes that result in benefits to human wellbeing; De Groot et al. 2002) that carry high ecosystem and societal value (Costanza et al. 1997; Orth et al. 2006; Cullen-Unsworth et al. 2014; Nordlund et al. 2016). Seagrasses enhance ecosystem productivity by creating structure that serves as habitat for species throughout the food web, and their high primary productivity serves as the basis of food webs through direct herbivory and the detrital cycle (Hemminga and Duarte 2000a; Green and Short 2003). Seagrass blades further enhance productivity in the coastal zone by attenuating wave and current forces, which increases nutrient retention from terrestrial run-off and tidal input and minimises particle resuspension (Ward et al. 1984; Gacia and Duarte 2001). These nutrients become bioavailable and may be processed by seagrass themselves and returned to the sediment during senescence or exuded back into the system via their roots and rhizomes (i.e., subterranean stems; Ziegler and Benner 1999; Aoki et al. 2020).

Alternatively, nutrients remain in the sediment (Mazarrasa et al. 2018). The anoxic sediment in seagrass meadows slows decomposition, prolonging nutrient retention, where it can remain buried for millennia (Mateo et al. 1997).

As a result of their various ecosystem functions, seagrass meadows provide numerous ecosystem services, defined as the direct and indirect benefits to human wellbeing (De Groot et al. 2002). These ecosystem services include subsistence harvest for small scale fisheries and contributing to fisheries productivity across the globe (Unsworth et al. 2018), enhancing shoreline stability, filtering nutrients, and offsetting carbon dioxide (CO_2) emissions by sequestering carbon (Duarte et al. 2013; Duarte and Krause-jensen 2017). In fact, seagrass meadows have been estimated to incorporate carbon into sediments up to 40 times faster than terrestrial systems (McLeod et al. 2011), amounting to an estimated 19.9 Petagrams (Pg) (or a more conservative estimate of 4.2 to 8.4 Pg) of organic carbon sequestered globally (Fourqurean et al. 2012).

Despite their recognized importance, seagrass meadows are declining globally, and at alarming rates (Orth et al. 2006; Waycott et al. 2009; Short et al. 2011). Based on a review of 215 studies, global loss of seagrass areal extent is estimated to be at least 29% since 1879 and at an accelerating rate of 110 km^2 yr^{-1} since 1980 (Waycott et al. 2009). Their position along the coast and adjacency to freshwater outflows exposes them to numerous anthropogenic pressures (Duarte 2002; Lotze et al. 2006). Seagrass meadows are pertinent examples of the destruction caused by coastal development and nutrient enrichment (Burkholder et al. 2007; Lefcheck et al. 2018). Excess nutrients promote phytoplankton or macroalgae blooms that outcompete seagrass for light, causing seagrass to suffocate due to contaminant and induced hypoxia. Other threats to seagrass include increasingly prevalent invasive species, such as European green crab (*Carcinus maenas*), which cut blades and uproot shoots, damaging meadows (Malyshev and Quijón 2011; Matheson et al. 2016), and biofouling species such as tunicates, which adhere to seagrass blades damaging them and inhibiting photosynthesis (Wong and Vercaemer 2012; Long and Grosholz 2015). More direct human activities, such as mechanical disturbances including boat scouring, dredging, and anchoring have also been linked to fragmentation and degradation of seagrass meadows (Zieman 1976; Erftemeijer and Robin Lewis 2006; Orth et al. 2006; Unsworth et al. 2017). Resulting scours can also facilitate the colonization of fast-growing invasive algal species, slowing seagrass recovery in previously disturbed systems (Cullen-Unsworth and Unsworth 2016). Additionally, coastal development can result in destruction of seagrass habitats by altering sediment and nutrient loading and by replacing natural shorelines with infrastructure, which undermines the capacity for seagrass meadows to migrate or expand spatially (Lotze et al. 2006). Finally, climate change alters freshwater inflow via shifts in precipitation regimes, causes thermal stress and sea-level rise, and enhances wave energy that damages coastal habitats (Harley et al. 2006; Bindoff et al. 2019). Sea-level rise coupled with coastal development, decreases the number of shallow environments with sufficient light penetration for seagrass to grow (i.e., coastal squeeze) (Orth et al. 2006; Tang and Hadibarata 2022). These threats can be synergistic (co-occur) and compounding (repeated before recovery), favouring fast-growing species and potentially fragmenting meadows and homogenizing communities (Thrush et al. 2008). Considering the ecosystem functions and services seagrasses provide (Costanza et al. 1997; Orth et al. 2006; Cullen-

Unsworth et al. 2014; Nordlund et al. 2016), such threats to seagrass meadows can have cascading effects on broader socioecological systems, prompting a need to manage for seagrass conservation.

1.2 Seagrass management challenges due to knowledge gaps

Following the Paris Climate Agreement in 2015, there is growing interest in using nature-based solutions to reduce atmospheric and oceanic CO_2 concentrations, to which seagrass can contribute if managed effectively (Duarte et al. 2013; Cooley et al. 2022). However, a significant challenge of seagrass management is evaluating trade-offs between economic development, conservation, and restoration (Daily et al. 2009; McShane et al. 2011). In some cases, ecosystem services have been attributed to a monetary value, allowing direct comparison between economic loss associated with seagrass meadow perturbation and economic gains from coastal development activities (Barbier et al. 2011). For example, ecosystems services provided by seagrass globally have been valued at US$34,000 per hectare per year (Costanza et al. 1997; Short et al. 2011). Although this approach enables seagrass to be evaluated according to human benefits, it involves extrapolating small scale quantifications of ecosystem services to a larger scale by assuming that ecosystem functions and services increase linearly by unit area (Dewsbury et al. 2016). However, such estimates have a high degree of uncertainty given that seagrasses have indirect socio-economic value via their ecosystem services, and the provision of ecosystem services is neither static nor uniform across regions, varying within and between seagrass meadows according to species, geographic region, and structural complexity (Barbier et al. 2008; Koch et al. 2009; Nordlund et al. 2016). Therefore, conservation efforts would benefit from identifying functional traits that promote ecosystem functions and subsequent services (Short et al. 2002; Unsworth et al. 2019a).

Globally, there are currently 13 recognized seagrass genera which vary in length, width, and density within and among species (Hemminga and Duarte 2000a; Boström et al. 2006; Nordlund et al. 2016). Meadows also vary in structural complexity, defined by three-dimensional physical attributes (e.g., height, density, patchy) and biodiversity (i.e., monospecific versus multiple species). Heterogeneity in structural complexity can be observed at various scales, such as the shoot scale, where seagrass shoots can vary in length and width, and at the meadow scale, where some meadows can be dense and continuous while others are sparse and patchy (homogenous areas of seagrass interspersed with unvegetated or macroalgae areas). Heterogeneity is further compounded by variability in the surrounding physical environment, including sediment composition, currents, and oceanographic properties (Thom et al. 2003a; Boström et al. 2006). Consequently, seagrass meadow structural complexity interactions with the physical environment affects ecosystem functions, which underpin the provision of ecosystem services. For example, more heterogeneous meadows tend to harbour higher biodiversity (Boström et al. 2006; Jones et al. 2021; further discussed in **Chapter 3**). In contrast, patchy meadows tend to support other ecosystem services less effectively, such as bank stabilization and carbon sequestration (Ricart et al. 2015; Oreska et al. 2017; further discussed in **Chapter 4**). Although studies have focused on relating seagrass meadow structural complexity to the provision of ecosystem services, there remain significant knowledge gaps on seagrass functions and resulting ecosystem services (Nordlund et al. 2018a).

The current global extent of seagrass is unknown, as few seagrass meadows have been mapped globally (Unsworth et al. 2019a; Mckenzie et al. 2020). Instead, estimates of seagrass status are based on ranges of distribution rather than maps of extent (e.g., (Waycott et al. 2009; Murphy et al. 2021). Studying seagrass meadows and their ecosystem services is significantly limited as maps, which serve as effective analysis and communication tools, are not widely available to scientists, policy-makers, and managers, and it is difficult to map meadows that are submerged. Maps are useful for understanding where seagrass meadows are located, where changes are occurring and at what rates, and can be used to estimate the provision of ecosystem services at various scales (e.g., meadow scale vs. regional scale vs. global scale, discussed in **Chapter 2**).

While conservation research aims to influence the use of coastal systems and policies to preserve these systems, limited general public awareness of the benefits of seagrasses reduces support for management decisions prioritising seagrass conservation (Bennett 2016; Lotze et al. 2018; Unsworth et al. 2019a). Seagrass meadows have generally received little media attention compared to other coastal habitats (i.e., salt marshes, mangroves, and coral reefs; Duarte et al. 2008), and public awareness of ecosystem benefits varies among individuals depending on experiences, interests, and lifestyles (Orth et al. 2006; Bennett 2016). Therefore, there is considerable need for improved mobilization of seagrass knowledge among experts (e.g., seagrass scientists) and non-experts (e.g., general public and politicians) (Orth et al. 2006; Nordlund et al.

2018a; Unsworth et al. 2019a). Improved communication among experts and non-experts could enhance awareness of seagrass distribution, the benefits they provide, and the threats to meadows, which could influence non-expert understanding and perspective of decisions affecting seagrass conservation.

1.3 Seagrass in Canada

Canada has the longest coastline in the world, where eelgrass (Z*ostera marina*) is the dominant species of seagrass along all three coastlines (Murphy et al. 2021). Eelgrass spatial extent is restricted to habitats with sufficient light penetration and sufficient nutrients availability (Hemminga and Duarte 2000a; Murphy et al. 2021). Growing in estuarine environments, eelgrass tolerate salinity ranges between 5 – 35 psu and temperature ranges between -1.5 – 30°C, with 10 – 25°C being optimal for growth (Murphy et al. 2021). Eelgrass meadows along the Pacific and Atlantic coastlines are mostly perennial and, although they undergo sexual (i.e., seed propagation) and asexual (i.e., cloning) reproduction, sexual reproduction is optimal at approximately 20°C and generally only occurs in up to 10% of the shoots.

To date, most of the eelgrass research in Canada has occurred along the Pacific and Atlantic coasts (e.g., Wong and Dowd 2015; Postlethwaite et al. 2018; Wong and Kay 2019; Prentice et al. 2020). Coinciding with global trends, eelgrass in Canada is declining mostly due to nutrient loading and invasive species (e.g., European green crab and biofouling species including golden star tunicates (*Botryllus schlosseri*)) (Murphy et al. 2019, 2021). According to the limited baseline data available through Environment

Climate Change Canada, Murphy et al. (2021) found that much of the decline along the Pacific coast has been reversed via restoration initiatives, leaving 93% of meadows either restored, stable or increasing. In contrast 31% of meadows in Atlantic Canada are still declining, potentially due to less active restoration efforts compared to the Pacific coast.

Eelgrass research in Atlantic Canada has included studies examining anthropogenic threats to eelgrass meadows, such as aquaculture (Cullain et al. 2018b) and eutrophication (Schmidt et al. 2017; McIver et al. 2019), examining the contribution of eelgrass meadows to biodiversity (e.g., Cullain et al., 2018; Wong & Dowd, 2015; Wong & Kay, 2019) and offshore fisheries recruitment (McCain et al. 2016), and developing human impact metrics to improve understanding of human activity on eelgrass meadows (Murphy et al. 2019, 2022). In Newfoundland and Labrador, extensive research on the ecological importance of eelgrass meadows has been ongoing for over 25 years in Newman Sound, a coastal fjord located on the northeastern coast of Newfoundland. These studies have predominantly demonstrated relationships between eelgrass meadow structure on particular fish species and fish communities. For instance, eelgrass research in Newman Sound has shown the importance of eelgrass as a year-round nursery habitat for juvenile Atlantic cod (*Gadus morhua*) (Gotceitas et al. 1997; Cote et al. 2004; Geissinger et al. 2022); an economically and culturally valuable species. Additionally, these studies have shown eelgrass meadows can increase juvenile Atlantic cod density (Thistle et al. 2010; Warren et al. 2010), reduce predation risk (Gorman et al. 2009), and enhance fish growth (Renkawitz et al. 2011). Together, eelgrass research conducted in Newman Sound shows that eelgrass meadow function as fish habitat varies according to meadow traits. Overall, the longevity and significance of eelgrass research in Atlantic Canada contributed to the designation of eelgrass as an ecologically significant species by Fisheries and Oceans Canada (DFO 2009), representing governmental recognition that perturbations to eelgrass meadows have a significant effect on other species and ecosystem processes.

Research on spatial variability in the provision of ecosystem services by eelgrass meadows in Canada is still preliminary, and consequentially, so is our understanding of traits underpinning this variability. Expanding research efforts to different regions with different oceanographic and anthropogenic influences, while examining different fish communities and ecosystems functions, will improve current understanding of the traits driving variability in ecosystem functions both locally and globally. Being a boreal system, Newfoundland and Labrador differs from much of coastal Canada, making it an important coastline to study.

This thesis focuses on eelgrass meadows in Placentia Bay, on the southeastern coast of Newfoundland. In 2017, the Government of Canada launched, a coastal restoration fund investing towards the preservation and restoration of coastal ecosystems as a part of the national Ocean Protection Plan (DFO 2020; Government of Canada 2022a). Placentia Bay was identified among the priority areas in Newfoundland and Labrador, and eelgrass restoration was one of the priority activities (DFO 2019, 2021a). Placentia Bay is home to the largest oil handling port in Canada and a commercial nickel processing plant, hosts some of the highest traffic waterways in Canada, including daily ferry crossings between Newfoundland and Nova Scotia from June to September, and will soon host numerous large salmon farming net pens. Additionally, Placentia Bay contains a commercial and recreational Atlantic cod fishery (NFAO division 3Ps) that has persisted for centuries and is of vital importance to the area (Robichaud and Rose 2006; Gattuso et al. 2013; Schrank and Roy 2013; DFO 2021b). In general, Newfoundland is one of the few areas in Canada that eelgrass status is not declining (Murphy et al. 2021). However, the introduction of European green crab into Placentia Bay in 2007 has resulted in considerable (50-100%) degradation of eelgrass meadows in the system, which coincided with a nearly simultaneous 10-fold decline in fish abundance at study sites (Matheson et al. 2016). On-going Coastal Restoration Fund efforts include mitigating the spread of European green crab into other coastal regions and transplanting eelgrass to promote meadow recovery.

1.4 Thesis objectives

In an era of rapid environmental change and growing anthropogenic pressure, threats to coastal ecosystems including eelgrass are becoming more prominent and necessitating conservation actions (Cullen-Unsworth and Unsworth 2018). The overarching aim of my thesis is to contribute to the collective understanding of eelgrass ecosystem services and the meadow traits underpinning the provision of these services. In doing so, my thesis contributes recommendations that can help focus management efforts of these highly valuable species. This thesis draws from a range of disciplines spanning mapping eelgrass meadows using remote sensing technology (**Chapter 2**), *in-situ* surveys (**Chapters 3-4**), and a public perception survey (**Chapter 5**). The resulting diverse perspectives of eelgrass enabled me to approach key research gaps important to eelgrass conservation, including mapping eelgrass, quantifying ecosystem services, identifying meadow structural traits that enhance those ecosystem services, and comparing the perception of eelgrass ecosystem services between experts and non-experts.

First, in **Chapter 2,** I used a remotely piloted aircraft system (RPAS) and supervised image classification procedures to map three eelgrass meadows in Placentia Bay. Doing so enabled me to describe the structural complexity of each meadow and relate it to the provision of ecosystem services in **Chapters 3 and 4**. Additionally, by collecting seasonal RPAS surveys and comparing resulting maps to conventional survey methods (i.e., snorkel transect surveys), I was able to evaluate the reproducibility of RPAS surveys in temperate systems and contribute recommendations for future monitoring using this increasingly popular technology.

Chapter 3 and **Chapter 4** applied results generated from the maps in **Chapter 2** to test the hypothesis that the provision of ecosystem services is related to meadow structural complexity. Specifically, in **Chapter 3**, I evaluated the contribution of eelgrass as a fish habitat by relating fish species richness and diversity in life history traits to eelgrass meadow structural traits and oceanographic properties. **Chapter 4** focused on the role of eelgrass in the coastal filter, an ecosystem function that maintains water quality by removing nutrients such as nitrogen from the water column and stores carbon in the sediment. Similar to **Chapter 3**, I related the role of eelgrass in the coastal filter according to eelgrass meadow structural traits and oceanographic properties, and extrapolated estimates of nutrients stored in the surface sediment to the meadow scale.

Whereas the two previous chapters focused on quantifying the provision of ecosystem services by eelgrass meadows in Placentia Bay, I designed **Chapter 5** to describe the perception of eelgrass by Canadian Atlantic coastal communities, including their perception of eelgrass status, ecosystem services, and management strategies. I explored ecosystem services relevant to coastal community members living in Atlantic Canada, exposing whether knowledge mobilization of the value of eelgrass ecosystem services is effective, and revealing whether there is public support behind eelgrass conservation.

Finally, in **Chapter 6**, I outlined the general conclusions and highlighted the major contributions of my research toward advancing current understanding of eelgrass ecosystem services, which includes a comparison of eelgrass meadow structural and environmental traits related to eelgrass ecosystem functioning measured in **Chapters 3 and 4**. Overall, this thesis provides region specific conclusions relevant to Atlantic Canada eelgrass meadows, but also contributes to the growing global characterization of the variability in eelgrass meadow functioning and resulting ecosystems services.

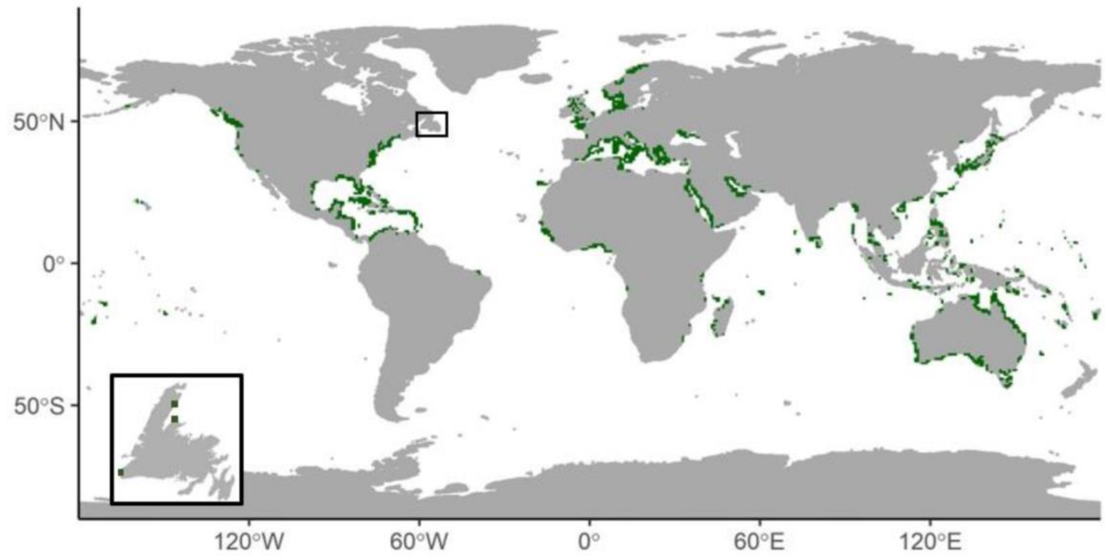

Figure 1.1: Map showing the global distribution of seagrass (green) according to data acquired from the United Nations Ocean Data Viewer database (UNEP-WCMC 2018). Data shows distribution of seagrass meadows but does not capture all known seagrass meadows along global coastlines. Black box in seagrass panel delineates Newfoundland, Canada.

Chapter 2: The reproducibility of remotely piloted aircraft systems to monitor seasonal variation in submerged seagrass and estuarine habitats

2.1 Abstract

Seasonal variation in seagrass growth and senescence affects the provision of ecosystem services and restoration efforts, requiring seasonal monitoring. Remotely piloted aircraft systems (RPAS) enable frequent high-resolution surveys at full-meadow scales. However, the reproducibility of RPAS surveys is challenged by varying environmental conditions, which are common in temperate estuarine systems. I surveyed three eelgrass (*Zostera marina*) meadows in Newfoundland, Canada, using an RPAS equipped with a three-colour band (red, green, blue [RGB]) camera, to evaluate the seasonal reproducibility of RPAS surveys and assess the effects of flight altitude (30-115 m) on classification accuracy. Habitat percent cover was estimated using supervised image classification and compared to corresponding estimates from snorkel quadrat surveys. My results revealed inconsistent misclassification due to environmental variability and low spectral separability between habitats. This rendered differentiating between model misclassification versus actual changes in seagrass cover infeasible. Conflicting estimates in seagrass and macroalgae percent cover compared to snorkel estimates could not be corrected by decreasing the RPAS altitude. Instead, higher altitude surveys may be worth the trade-off of lower image resolution to avoid environmental conditions shifting mid-

survey. I conclude that RPAS surveys using RGB imagery alone may be insufficient to discriminate seasonal changes in estuarine subtidal vegetated habitats.

2.2 Introduction

Seagrasses occur along the coastlines of every continent except for Antarctica (Short et al. 2001) and support numerous ecosystem functions and services including food provision, water purification, fish habitat, and carbon sequestration (Nordlund et al. 2016). Global declines in seagrass meadows and resulting loss of ecosystem functions and services are major concerns in conservation ecology (Barbier et al. 2011; Orth et al. 2006; Salinas et al. 2020; Waycott et al. 2009; Worm et al. 2006). Increasing efforts have been made globally to monitor and restore seagrass meadows (Orth et al. 2020; Tan et al. 2020) and to quantify the services they provide (Nordlund et al. 2018, 2016). Strong seasonality in light availability and other environmental conditions (e.g., freshwater influx, temperature) in cold-temperate estuarine regions results in marked periods of growth and senescence in seagrass (Hemminga and Duarte 2000). Such seasonal variation can affect the provision of ecosystem functions and services (Sonoki et al. 2016) and the success of restoration efforts (Li et al. 2014; Zimmerman et al. 1995). This supports the need for seasonal monitoring of seagrass meadows (Björk et al. 2008; Kirkman 1996), which may further be used to determine the optimal season for restoration actions (Li et al. 2014; Zimmerman et al. 1995) and for annual monitoring.

Seasonal monitoring of seagrass and adjacent estuarine benthic habitats improves understanding of changes in the meadow and the provision of ecosystem services, but requires methods that can detect fine-scale seasonal variability in cover and extent of the different benthic habitats (Chand and Bollard 2022), while surveying at the meadow-scale (often several hectares). These methods must also be reproducible, meaning they produce similar resolution and accuracy across surveys. Numerous approaches have been used for seasonal monitoring of seagrass meadows including wading/snorkel/SCUBA surveys (Cho et al. 2017; Fourqurean et al. 2001; Short et al. 2006), aerial photos (Reise and Kohlus 2008), satellite imagery (Lyons et al. 2013), and acoustic surveys (Sonoki et al. 2016). Remote sensing applications for seagrass monitoring are generally used to measure seagrass extent (Lyons et al. 2013), whereas wading/snorkel/SCUBA approaches reveal smaller scale and higher resolution details such as shifts in percent cover of seagrass, shoot density, and species composition (i.e., presence of macroalgae; Fourqurean et al. 2001; Short et al. 2006). More recently, remotely piloted aircraft systems (RPAS; i.e., drones) have been applied to monitor seasonal variation in seagrass extent and structure (Chand and Bollard 2022; Krause et al. 2021) due to their ability to collect high resolution images frequently and at a relatively low cost and their potential to automate part of the work (Colefax et al. 2018; Joyce et al. 2018). By reducing monitoring costs, RPAS present a promising approach for seagrass monitoring because seagrass monitoring is widespread and conducted by groups that are resource and time limited, including academics, non-profit, and government entities seeking to optimize monitoring resources. However, studies on seasonal reproducibility of RPAS did not include delineation of other adjacent estuarine habitats (e.g., other species of submerged aquatic vegetation), which can be challenging to spectrally separate (Duffy et al. 2018; Tait et al. 2019), and focused RPAS surveys on limited portions of a meadow. Examining whether full-meadow scale seasonal RPAS surveys can reliably detect changes in seagrass extent, percent cover, and differentiate seagrass from other habitats would determine whether

RPAS effectively bridge the gap between remote sensing and wading/snorkel/SCUBA surveys.

To detect seasonal changes in seagrass, RPAS surveys must be reproducible. However, a major challenge with RPAS surveys is that image quality quickly diminishes in less than optimal environmental conditions (e.g., cloud cover, wind, turbidity, high-tide), challenging seagrass identification (Joyce et al. 2018; Nahirnick et al. 2019a, 2019b). These environmental changes can shift within minutes/hours and mid-survey (e.g., tide, cloud cover, sun angle) as well as over longer time periods, including seasonally and annually. Additionally, seagrass blades may fold over at low tide or when there is a fast current, increasing the likelihood of overestimating seagrass density. While recent studies have provided roadmaps of ideal environmental conditions for RPAS surveys of seagrass (e.g., Joyce et al. 2018; Nahirnick et al. 2019b; Tait et al. 2019; Yang et al. 2020), studies evaluating the efficacy of surveys have generally focused on one-time occurrences in tropical regions (e.g., Ellis et al. 2020) or portions of a meadow (Barrell and Grant 2015; Duffy et al. 2018; Ellis et al. 2020; Konar and Iken 2018; Krause et al. 2021). In temperate regions, high environmental variability, including rapid shifts in cloud cover, wind, and chemistry of estuarine waters (e.g., tannins), challenges RPAS surveys (Nahirnick et al. 2019a, 2019b). The source and frequency of environmental variability in temperate estuarine systems often differ among seasons, making seasonal monitoring even more challenging as it can be difficult to collect comparable images. For instance, seasonal effects include higher rainfall in the fall and snowmelt in the spring, whereas daily variation includes changing water levels due to tide and rainfall and varying tannin concentrations depending on riverine discharge. Therefore, an evaluation of survey accuracy and reproducibility in such systems is necessary if RPAS are to be used to monitor changes in habitat extent, percent cover, and adjacent benthic habitat over time.

Detecting fine-scale seasonal changes in seagrass meadows requires collecting high spatial resolution surveys. RPAS image resolution is inversely proportional to altitude, and fewer details in images collected at higher altitudes can complicate habitat classification and survey reproducibility (Seifert et al. 2019). However, increasing survey altitude reduces flight time as larger areas are covered per image, which limits the risk of environmental conditions such as sun angle and tide, which change within minutes/hours, from changing mid-survey (Joyce et al. 2018) and enables more frequent surveys. Furthermore, varying flight altitude may affect the reproducibility of RPAS surveys in multiple ways. Ellis et al. (2020) showed the effect of altitude on image classification depended on habitat when surveying at increasing altitude, presumably due to different levels of spectral separability among habitats. Sand cover estimates increased with altitude, whereas seagrass estimates decreased, and mangrove, coral, and open water estimates were unaffected. These differences highlight the need to better understand the trade-offs associated with altitude, including how they relate to the structure of the meadow (e.g., patchy vs. continuous) and location in the meadow (i.e., edge vs. middle) to conduct reproducible seasonal surveys of seagrass meadows.

The first objective of this study was to test the reproducibility for RPAS to monitor seasonal changes in eelgrass (*Zostera marina*) meadows and adjacent benthic estuarine habitats in cold-temperate ecosystems. This represents the first study to evaluate the capacity of RPAS surveys to detect seasonal (i.e., summer vs. fall) variation in meadow extent, percent cover, and macroalgae cover across multiple sites of relatively large area (~50 ha). I compared orthomosaics and image classification accuracies across surveys to assess the reproducibility of RPAS for estimating seasonal changes in seagrass extent in three sites. RPAS estimates of habitat percent cover and species composition were compared to complementary snorkel quadrat surveys to evaluate whether both methods yielded similar seasonal trends in eelgrass and macroalgae percent cover. Finally, since flight altitude implies trade-offs between image resolution and survey duration, my second objective was to evaluate the effects of flying at a high altitude (e.g., 30 m vs. 115 m) on estimates of seasonal changes in percent cover.

2.3 Methods

2.3.1 Study sites

I surveyed three sites with eelgrass meadows in Placentia Bay, Newfoundland: North Harbour, Swift Current, and Baie de l’Eau (Figure 2.1). North Harbour and Baie de l’Eau are shallow meadows, growing to a maximum depth of <1 m (below chart datum). The eelgrass meadow in North Harbour is divided into two main patches, whereas the Baie de l’Eau meadow is patchy throughout. The Swift Current meadow is more continuous, where eelgrass maximum depth reaches 0-2 m (below chart datum) depending on the section of the meadow. Macroalgae, predominantly *Fucus* spp., *Chorda filum*, *Ascophyllum nodosum*, and *Chondrus crispus* also occur in each meadow.

2.3.2 RPAS surveys

I conducted two surveys per site in 2020: one in the summer (July 6-22) and one in the fall (September 21-October 13) (Table 2.1). Markers for ground control points (GCPs) and check points (CPs) were placed onshore surrounding the eelgrass meadows (see *2.3.4 RPAS data processing* for application; see Appendix A for methods of deploying GCPs and CPs).

RPAS surveys were conducted using a DJI Matrice 210 RTK equipped with a 24 mm lens Zenmuse X7 camera and a polarized lens. Flight plans were executed using the DJI Pilot application. White balance, shutter speed, and ISO were set prior to each survey while the RPAS hovered at 115 m altitude (same as the survey altitude; see Appendix A Table S2.1). I conducted the surveys when there was no cloud cover (0%) and in low wind conditions (i.e., ≤10 km/h) according to the European Centre for Medium-Range Weather Forecasts model (www.windy.com), while also avoiding days following a rain event when turbidity would be elevated. Such weather combinations are uncommon in Newfoundland; therefore, I could not control for tidal height among surveys (Table 2.1). Instead, I prioritized consistent reflectance across the survey, which is necessary to apply automated classification during post-processing. I also conducted the surveys during early morning or late afternoon (Table 2.1), when the sun was between 20-40° to minimize glare (Mount 2005; Nahirnick et al. 2019b; Ellis et al. 2020), and to avoid wave-induced disturbances. Only Swift Current was surveyed in the afternoon because it has a short fetch. For each site survey, the RPAS was programmed to fly at 115 m altitude while moving 6 ms^{-1}, and to capture photos continuously with the camera nadir facing. Images were collected with 80% front overlap and 70% side overlap.

2.3.3 Collecting ground-truth data

I collected GoPro images to create training and validation data for the RPAS supervised image classification. This involved collecting images of the seafloor throughout the site using a GoPro camera and georeferencing these images using a handheld GPS (Garmin etrex 20xTM). The images were analysed to identify the dominant habitat (eelgrass, macroalgae, unvegetated) then used to train and validate the image classification model of the RPAS survey (see *2.3.4 RPAS data processing*). Training and validation data were collected for each site within a week of the RPAS survey.

Next, I collected snorkel quadrat survey data to evaluate the reproducibility of the RPAS survey to measure eelgrass and macroalgae percent cover. For the snorkel transect survey, I marked six transects in each site using rebar embedded into the shore and georeferenced using a GPS. Transect locations were chosen such that two intersected the middle, two intersected the edge, and two were outside of the meadows (Appendix A Figure S2.1). Snorkel transects followed a 50 m lead line marked at 10 m intervals starting 20 m from the water's edge to mark the quadrat placement (Appendix A Figure S2.1). Using a 1 m^2 quadrat divided into a 10 cm × 10 cm grid, eelgrass and macroalgae densities were estimated as the percentage of grid cells within the quadrat with shoots ($n_{quadrat/site} = 24$). If a grid cell had both eelgrass and macroalgae, it was counted as both. If no eelgrass or macroalgae was present, the grid cell was classified as unvegetated. Similar to the RPAS surveys, I conducted two snorkel quadrat surveys for each site, once in the summer and again in the fall. All snorkel quadrat surveys were performed by the same snorkeller and within a month of the RPAS survey.

2.3.4 RPAS data processing

Orthomosaics were generated using Agisoft Photoscan (v.1.4.5). I divided the GCP/CP markers to use 70-80% of the markers to optimise the position accuracy of the orthomosaic, and the remainder to evaluate error in the orthomosaic (Table 2.1). Orthomosaics were exported at a 10 cm × 10 cm pixel resolution to match the size of the grid cells in the quadrat used during the snorkel survey (see *2.3.3 Collecting ground-truth data*), which also reduces the pixel variability in the orthomosaics.

Orthomosaics were analyzed separately using random forest supervised image classification via the "superClass" function in the RStoolbox (v. 0.2.6.; Leutner et al. 2019) package in RStudio (v. 1.2.5033; R Core Team, 2022). I defined the training data according to the red, green, and blue (RGB) colour composites for the pixel associated with each training point (Figure 2.2). This was done by projecting the coordinates of the GoPro imagery onto the orthomosaic in ArcMap (v. 10.7). Given that the GPS used to georeference the training data has an accuracy of 3.65 m, I inspected the 100 ± 20 training points collected for each RPAS survey to ensure that the habitat attributed to the point matched the location of the point (e.g., eelgrass was not in the middle of unvegetated habitat). If a point was obviously wrong, it was removed. Training data were then supplemented with additional training data to obtain 50 training points per habitat. These training points were created by selecting pixels on the orthomosaic from easily identifiable habitats and recording location and the associated colour composites. To minimise subjectivity and potential misclassification, I re-evaluated the additional training data using kernel density estimates of the GoPro collected training data, where pixels were labelled according to the habitat with the highest kernel density estimate. Only pixels where the visual classification and kernel density estimate agreed were used to supplement the GoPro training data for the supervised image classification. Because macroalgae was sparse in North Harbour and Swift Current in fall, fewer training data could be created (min $n_{macroalgae}$= 26). I then assigned a 10 cm buffer to the training data to cover roughly the same area as the GoPro images and to account for pixel variability within each habitat type.

Finally, I used kernel density curves of the training data to identify the number of classes to include in the model (Figure 2.2; see Appendix A Figure S2.2 for kernel density curves). If a curve was bi-modal, I divided the habitat into two separate classes (e.g., exposed eelgrass and submerged eelgrass) to optimise the model classification process (Lillesand and Kiefer 2000). I applied 80% of the training data to build the image classification models and the other 20% for model validation. I then refined the models using a majority filter, which classified pixels while accounting for the class and mode of the adjacent pixels. Each model was evaluated using a confusion matrix, user accuracy, and Cohen’s Kappa accuracy (i.e., model accuracy while accounting for the probability that a pixel was classified correctly by chance; Rosenfield and Fitzpatrick-Lins 1986). These metrics were calculated using the “validateMap” function in RStoolbox. Habitats that were divided in two classes according to the bi-modal kernel density curves were then merged back as one habitat (e.g., “submerged” and “exposed” eelgrass became “eelgrass”). I then assessed seasonal changes in eelgrass area coverage between summer and fall by comparing the differences in eelgrass pixels between seasons for each site. Eelgrass area coverage was calculated by multiplying the number of eelgrass pixels by their size (0.01 m^2), and the percent change between seasons was then calculated.

2.3.5 Comparing RPAS and snorkel transect surveys

I assessed the differences in estimates of benthic habitats between RPAS and the snorkel transect surveys by cropping 1 m^2 quadrats from the classified RPAS model and calculating the percentage of pixels from each habitat class. Quadrat polygons were created in ArcMap mimicking the approach used in the field for the snorkel transect survey. While this approach does not guarantee that locations of the digital quadrats exactly matched those of the snorkel survey, it did allow similar portions of seabed to be compared. I used zero-inflated Poisson (ZIP) regression models to evaluate seasonal changes in eelgrass cover, one per survey method, to relate eelgrass and macroalgae estimates of cover to season, site, and location. These models were used to determine whether both methods indicated similar seasonal changes in eelgrass cover.

2.3.6 Assessing altitude trade-off

Two tests were conducted to evaluate the effects of increasing altitude on benthic classification during RPAS surveys. I conducted these tests at Capelin Cove, a sub-site within North Harbour (Figure 2.1). The first test compared habitat percent cover from

RPAS surveys conducted at four altitudes (25, 50, 100, and 115 m) with percent cover from snorkel transect surveys – hereafter referred to as the Capelin Cove test. RPAS surveys were conducted sequentially on the same day (Table 2.1). To avoid motion blur, flight speeds were decreased at lower altitude (Table 2.1). There were no GCPs or CPs available for Capelin Cove. I used training data and surveyed two transects (one inside and one edge, $n_{quadrat} = 8$). Otherwise, I used the same procedures for both the RPAS and the snorkel transect surveys previously described, including exporting imagery to 10 cm resolution.

The second test compared classification estimates from RPAS images of a submerged quadrat taken at increasing altitudes – hereafter referred to as the quadrat altitude test. I positioned the submerged quadrat to intersect an eelgrass, macroalgae, and unvegetated boundary (Figure 2.3) and collected the RPAS images of the quadrat at ~3 m altitude intervals from 30-121 m (Appendix A Table S2.1). All photos were collected using the same camera settings and with the camera pointing nadir. For each photo, I used a 0.9 m × 0.9 m polygon centered within the quadrat to crop the images such that the quadrat itself (i.e., PVC pipe) would not be included in the image classification. Unlike the Caplin Cove test, image resolution was not altered (see Appendix A Table S2.1). The cropped images were then classified into the three habitat classes using a random forest unsupervised image classification approach using the “unsuperClass” function in RStoolbox and a majority filter. I calculated the percentage of pixels for each habitat and each altitude and compared these values to the percent cover of each habitat obtained from an underwater image of the submerged quadrat (Figure 2.3). Simple linear regression was used to evaluate the relationship between survey altitude and differences in percent cover of each habitat measured using the RPAS versus the underwater image.

2.4 Results

2.4.1 RPAS survey

The RPAS successfully surveyed macroscale eelgrass meadows while flying at 115 m altitude (Figure 2.1). According to the RPAS models, eelgrass extent in North Harbour decreased by 2.6% (-0.30 ha) between the summer and fall, Swift Current increased by 17% (2.1 ha), and Baie de l'Eau decreased by 23% (-5.5 ha) (Table 2.1).

Spectral separability varied among habitats and sites (Figures 2.1, S2.2), making eelgrass detection more challenging in some sites than others. Spectral separability was highest in North Harbour for summer and fall orthomosaics, which produced the most similar seasonal datasets among the sites. Baie de l'Eau had different levels of spectral separability between eelgrass and unvegetated cover between seasons, and Swift Current orthomosaics showed little separability between habitats in both seasons in areas where the eelgrass was submerged. These differences in spectral separability between sites were reflected in the supervised classification model accuracy, where the overall accuracy and the Cohen's Kappa accuracy were highest for North Harbour (Figure 2.4A, B), followed by Baie de l'Eau (Figure 2.4C, D) and Swift Current (Figure 2.4E, F) surveys, even though they were conducted under similar environmental conditions and low turbidity (Table 2.2, see Appendix A for methods of measuring turbidity). Eelgrass misclassification was inconsistent for all models and was highest for Swift Current (Table

2.3). Inconsistent misclassification negatively affected the reproducibility of the RPAS surveys, resulting in accuracies differing by >10 % between seasonal surveys for Swift Current and Baie de l’Eau (Figure 2.4). Additionally, inconsistent misclassification rendered it infeasible to distinguish between model confusion versus where, if any, micro/meso-scale changes in seagrass extent or cover occurred (Appendix A Figure S2.3).

In general, the RPAS survey models and the snorkel transect surveys yielded similar percent cover estimates. North Harbour RPAS estimates were most comparable to the snorkel estimates, followed by Baie de l’Eau, and then Swift Current (Appendix A Figure S2.4). Overall, the median absolute value difference in eelgrass percent cover between RPAS and snorkel quadrat estimates indicated that the RPAS yielded a ≥70% classification accuracy for most sites and locations (i.e., edge, middle, outside), with the exception of the inside transect for the Swift Current summer survey (~45%). Macroalgae estimates differed the least between the two methods, with a median RPAS accuracy ≥75% for all cases. Overall, location in the meadow did not have a clear effect on the differences in estimates between the two methods. Despite these similarities, the two methods yielded different seasonal trends in eelgrass and macroalgae percent cover (Figure 2.5). However, these differences were not apparent in the ZIP models, which suggested similar conclusions for both survey methods. Specifically, the RPAS estimates of eelgrass cover exhibited a limited effect of season (summer estimate 0.07% higher than fall) and no seasonal effect was detected by the snorkel method (Table 2.4). A similar trend was observed for macroalgae estimates (0.52%; see Appendix A Table S2.2). Both methods suggested similar variability in estimates of cover, where more variability in eelgrass cover occurred in the edge transects compared to inside (Figure 2.5).

2.4.2 Altitude trade-off

For the Caplin Cove test, photos collected at 25 m altitude did not align to generate an orthomosaic, likely due to low variability in texture and colours among images (Appendix A Figure S2.5A). Comparison between the other RPAS surveys and the snorkel transect survey estimates of habitat cover did not reveal a trend between habitat classification and increasing RPAS survey altitude for transects inside meadows (Figure 2.6). However, for edge transects, differences between RPAS and snorkel transect survey estimates of habitat cover decreased with increasing altitude for eelgrass and macroalgae. Inside transects were most similar between the two methods when the RPAS survey was conducted at 100 m altitude and most different when conducted at 115 m, but overall median values were similar (<5% difference). Therefore, in this first test, higher altitude surveys appeared to improve the accuracy of coverage estimates for the edges of eelgrass meadows and did not affect estimates inside the meadows.

For the quadrat altitude test, there was a positive correlation between altitude and differences in eelgrass cover estimated via the underwater image and RPAS images (Figure 2.7). Differences in eelgrass cover estimates increased by 0.09% m^{-1} altitude, increasing from a 19% difference at 30 m to 27% at 121 m (Figure 2.7). Meanwhile, estimates of macroalgae improved with increasing altitude. Macroalgae estimates were ~10% higher than the underwater imagery at lower altitudes, decreasing by 1.0% m^{-1}

altitude. Estimates of unvegetated cover decreased by 0.04% m^{-1} altitude, however these differences were not statistically significant.

2.5 Discussion

This study assessed the feasibility of conducting reproducible RPAS surveys to monitor the seasonal dynamics of eelgrass and adjacent benthic habitats at the meadow-scale (e.g., 50 ha) in a cold, temperate, estuarine ecosystem. My results demonstrate that the capacity of RPAS to detect seasonal variation in habitat percent cover is highly variable within and among sites. The two survey methods (i.e., RPAS and snorkel transects) used in this study detected a <1% seasonal change in eelgrass percent cover, suggesting negligible variation in seagrass cover and therefore, potentially negligible change in the provision of ecosystem services by eelgrass in Newfoundland between mid-summer and early-fall. Eelgrass in Atlantic Canada reaches peak growth in August before declining in the winter due to sea ice and storms (Murphy et al. 2021). Therefore, my study shows that annual monitoring of eelgrass during peak season could be extended until late September/early October. However, RPAS image classification was challenged by patchy, heterospecific, and deeper benthic habitats. Inconsistent misclassification rendered locating micro/meso-scale changes infeasible, potentially preventing me from identifying sections of the meadow where seasonal changes in extent and percent cover may have occurred. This would have implications for the reproducibility of any repeated monitoring using RPAS, whether it be seasonal or annual.

My results also showed that the effects of flight altitude on accuracy are not straightforward. Macro-scale (i.e., snorkel transect comparison) estimates of cover improved with increased altitude, whereas micro/meso-scale (i.e., submerged quadrat comparison) cover estimates varied depending on the habitat. Flying at higher altitude advantageously reduces survey time to the detriment of image resolution. However, given that accuracy was not necessarily reduced at higher altitude, I suggest that, when monitoring macro-scale changes in benthic estuarine habitats where the environmental conditions are frequently shifting within minutes/hours, the benefit of increased likelihood of successful survey (e.g., image stitching) outweigh the cost of collecting lower resolution imagery. This finding is applicable to any group seeking to use RPAS to monitor macro-scale changes in submerged, estuarine habitats.

2.5.1 Reproducibility

The reproducibility of RPAS surveys is likely limited by a combination of environmental factors. Successfully mapping eelgrass meadows using RPAS has been linked to weather and light penetrability (Joyce et al. 2018; Nahirnick et al. 2019a, 2019b). Although all surveys in my study were conducted in optimal weather conditions and all the sites were less than 5 m deep, depth was not consistent among surveys as I could not control for tide. Light penetration is reduced with increasing depth, such as high tide or deeper portions of a meadow. This is particularly the case for red wavelengths, which become absorbed or scattered, making deeper sites harder to survey (Duntley 1963; Tait et al. 2019). In shallow portion of the meadow, low tide causes seagrass blades to bend, which increases the likelihood of overestimating seagrass percent cover and extent. As a result, there is no universal ideal tidal height to survey seagrass using RPAS. The effect of tide on seagrass imagery varies depending on the meadow blade length and how much depth varies throughout the meadow. I did not have the data resolution to detect whether water tidal height caused the variability I observed, however neither did I observe any patterns in my results.

Turbidity, a common feature in coastal temperate regions due to freshwater influx and seasonal phytoplankton blooms, also inhibits light penetrability and is a common feature in coastal temperate regions (Babin et al. 2003; Duntley 1963). Turbidity was low for all surveys (Table 2) and therefore was unlikely to have driven the differences in accuracy. However, I did observe seasonal differences in the surface water colour, especially in the Baie de l'Eau fall survey (Figure 1C). This was likely caused by influx of tannin-rich freshwater, as observed by the red/brown color of the orthomosaic (Figure 1C), and potentially by the tidal amplitude difference between surveys (1.4 m compared to 0.2 m for the other two sites). Seasonal variation in freshwater influx and mixing generates unique interactions among light, depth, and colour. These interactions may have contributed to the seasonal variability in survey accuracy observed in my study.

As observed in other studies, spectral separability between habitats affected image classification (Lillesand and Kiefer 2000; O'Neill and Costa 2013; Tait et al. 2019; Ventura et al. 2018). This in turn affected the reproducibility of my RPAS eelgrass surveys. Spectral signatures showed instances of substantial spectral overlap between habitats, causing classification confusion. Spectral separability between eelgrass and unvegetated cover diminished at the transition from shallow to deep water, creating an erroneous eelgrass boundary between unvegetated habitat and deep water in both of my North Harbour models. However, this was not detected in the confusion matrix, which showed eelgrass classification errors stemming from unvegetated seabed and macroalgae. Therefore, I suggest that model accuracy estimates may be misleading and enforce the importance of refining/validating RPAS surveys with complimentary ground-level surveys. Furthermore, consistent with previous studies (e.g., Barrell and Grant 2015; Duffy et al. 2018; Nahirnick et al. 2019b), sparse habitats or edges were more difficult to differentiate than continuous habitat. This may be because habitats underwater are more likely to appear different in aerial imagery due to light refraction (Ellis et al. 2020; Joyce et al. 2018). Additionally, classification errors are more likely to occur at habitat boundaries, where spectral signatures of boundary pixels are composed of a mixture of habitat types (Woodcock and Strahler 1987), which generates pixels with intermediate tones, confusing the classification model. Thus, my results suggest that reproducible RPAS surveys of either deep (>5 m), patchy, or more heterospecific eelgrass meadows are more difficult to acquire and seasonal estimates of change may be more prone to error. Separating submerged aquatic vegetation into eelgrass and macroalgae classes likely explains the lower model classification accuracies in my study. Using multispectral sensors may facilitate the detection of submerged benthic habitats in estuarine environments (James et al. 2020; Su et al. 2006), but this is beyond the scope of my study.

Various post-processing workflows have been applied in the literature to classify remote sensing imagery (e.g., Murfitt et al. 2017; Duffy et al. 2018; Ventura et al. 2018;

Wilson et al. 2019; Schroeder et al. 2019). Most approaches include some form of manual classification to delineate features of interest, or to create training data *post-hoc* based on the analyst's interpretation of the system and imagery (e.g., Konar and Iken 2018; Ventura et al. 2018; Gonçalves et al. 2019; Nahirnick et al. 2019b). This introduces observer bias into the classification process, impacting the reproducibility of the survey. I present a method using kernel density plots to supplement training and validation data *post-hoc*, which minimizes analyst-induced bias. However, some subjectivity was still required to select training data, such as ensuring these data do not come from pixels falling on habitat boundaries (Lillesand and Kiefer 2000), and avoiding clustering training data to avoid overfitting sections of the model. My study only tested the reproducibility of RPAS surveys using RGB imagery without supplemental information. Supplementing training data with additional habitat-defining characteristics such as depth and optical texture or collecting multispectral imagery to separate habitats (e.g., Tait et al. 2019) would likely improve the reproducibility of RPAS surveys for monitoring submerged eelgrass meadows and adjacent estuarine habitat, and may be required when reproducibility is low.

2.5.2 Do results improve with altitude?

Terrestrial and coastal RPAS surveys have shown that lower altitude surveys enable more habitats to be distinguished in the imagery (Perroy et al. 2017; Duffy et al. 2018). However, I found that reducing survey altitude did not always improve agreement in estimates of submerged eelgrass and macroalgae percent cover between RPAS surveys and snorkel quadrat surveys. Full site surveys showed that the accuracy of RPAS estimates improved with altitude for the edge transects, while it was unaffected for the inside transects. This could be because finer details such as ripples and shadows on the surface were detected by lower altitude images, increasing spectral variability (Mount 2005; Woodcock and Strahler 1987) and potentially reducing accuracy. For continuous eelgrass meadows, such disturbances are likely minimal on inside transects at lower altitudes given that the pixels are from the same habitat type. In contrast, the edge of the eelgrass meadow is patchier. Therefore, intermediate spectral tones from multiple habitats in a pixel, and water disturbance will more likely distort habitat boundaries, altering apparent eelgrass coverage. At a higher altitude, noise from texture features such as ripples would have been reduced as lower resolution images smooth finer details and reduce spectral variability (Woodcock and Strahler 1987). Therefore, the accuracy of RPAS surveys of meadow edges or of patchy meadows may be improved in higher altitude surveys.

In contrast, the quadrat altitude test suggested that the effect of increasing altitude varied among habitats. Similar results were reported by Ellis et al. (2020) while flying a fixed wing RPAS at similar altitudes as my study. Reduced image resolution with higher altitude increases the number of pixels that encompass a mixture of habitat types, and thus the number of pixels with intermediate colour tones, which subsequently reduces classification accuracy (Woodcock and Strahler 1987). I could therefore expect that, in heterogenous meadows, higher altitude would decrease classification accuracy. While this was the case for eelgrass and macroalgae, classification of unvegetated habitat was less affected by changes in image resolution with changing altitude. This is likely because eelgrass and macroalgae have similar spectral signatures regardless of resolution, while unvegetated habitat was more spectrally separable from the other two habitat classes. Nevertheless, in all cases the effect of increasing altitude only changed the estimates of cover by up to 10%. Flying at higher altitudes helps survey larger scale meadows within limited battery life of the RPAS and reduces the risk of environmental conditions that change within minutes (e.g., sun angle, tide, cloud cover) from changing during the survey (Joyce et al. 2018). Therefore, in the case of large, submerged eelgrass meadows, the benefit of surveying at a higher altitude may outweigh the cost of collecting lower resolution imagery, especially given that images collected at lower altitudes can be more challenging to stitch into an orthomosaic.

2.5.3 Conclusion

Seasonal monitoring of seagrass meadow extent and adjacent estuarine habitats is important for coastal habitat management. In Newfoundland, seasonal changes in seagrass extent and cover would be more likely to be detected with survey periods starting earlier in the spring (e.g., April/May) after ice-melt and when eelgrass cover is low, then in the late summer/early fall (e.g., August/September). Issues of ice formation in the late fall/winter when eelgrass die-off (i.e., December) and increased riverine discharge due to snow melt in the spring, in addition to other varying environmental conditions (e.g., tide, wind, cloud), render seasonal monitoring using RPAS extremely challenging in north temperate environments. For these reasons, monitoring using RPAS in this region is optimal in summer/early fall months (i.e., July-early October), when eelgrass is the least patchy (i.e., peak growth) and environmental conditions are more conducive to RPAS surveys. Similar logic could be applied to other temperate regions as well.

Regardless of the monitoring period, recognizing the limitations of RPAS surveys is crucial for reliable monitoring. I show that sources of variability on RPAS surveys limit reproducibility and therefore limit how much RPAS can be relied on to detect fine-scale changes during management decision-making, including changes in percent cover of seagrass and adjacent benthic habitats. In my study, trends in seasonal changes in seagrass and macroalgae percent cover often differed between RPAS and snorkel transect surveys. Differences in tidal height may have contributed to the variability observed, however, this is a significant challenge and potentially a limitation if RPAS are to be used to monitor submerged coastal habitats in temperate regions, where low wind and no cloud conditions are rare. Supplementing imagery with texture data such as bathymetry maps, secchi depth, or multispectral imagery could help correct for depth and potentially help overcome reproducibility challenges but come at an additional cost and may be unfeasible for many monitoring groups. Overall, selecting whether to use RPAS surveys to monitor seagrass over time is question dependent. RPAS appear to be reliable for large scale surveys to detect macro-habitat characteristics, such as general extent and identifying meadow structure, and delineating vegetated versus unvegetated habitat in general. For example, edges and patchy areas should be monitored via snorkel while large, submerged seagrass meadows can be monitored using higher altitude RPAS imagery. In this case, increasing survey altitude helps mitigate the risk of environmental conditions shifting mid-survey, thereby offsetting the cost of obtaining lower resolution imagery.

Meanwhile, RPAS equipped with RGB sensors alone cannot distinguish between macroalgae and seagrass reliably, and estimates of fine-scale habitat changes, such as changes in species composition or eelgrass growth through time, should be interpreted with caution.

Table 2.1: Summary of remotely piloted aircraft system (RPAS) survey, including survey duration, number of ground control points (GCPs) and control points (CPs) used to create the orthoimage, survey coverage, flight altitude, flight speed, and tidal height. The number of GCPs/CPs and their placement were limited by tree cover and substrate that was stable yet penetrable by the rebar (see Appendix A for GCPs and CPs deployment). Total estimated eelgrass area (m) was calculated by classifying the RPAS imagery using supervised image classification with random forest analysis.

Site	Season	Sample date & time (day/month/year h:m)	GCPs/CPs	Survey area (ha)	Flight altitude (m)	Flight speed (ms^{-1})	Tide height (m)	Eelgrass area (ha)
Swift Current	Summer	06/07/2020 16:45-17:25	4/2	30.9	115	6	0.7	5.23
	Fall	21/09/2020 15:43-16:42	5/2	30.9	115	6	0.9	7.38
North Harbour	Summer	18/07/2020 9:19-10:17	5/3	52.3	115	6	1.7	5.76
	Fall	06/10/2020 9:29-10:42	5/3	52.3	115	6	1.5	5.46
Baie de l'Eau	Summer	22/07/2020 9:19-10:17	6/3	70.1	115	6	2.3	14.54
	Fall	13/10/2020 9:54-11:42	6/3	70.1	115	6	0.9	9.04
Capelin Cove	Summer	18/07/2020 10:30-10:40	-	2.7	25	1.3	1.3	-
Capelin Cove	Summer	18/07/2020 10:43-10:52	-	4.4	50	2.6	1.3	-
Capelin Cove	Summer	18/07/2020 10:22-10:27	-	3.2	100	5.2	1.3	-

Table 2.2: Median water nephelometric turbidity units (NTU) during each remotely piloted aircraft systems (RPAS) survey. Data were measured using a moored ECO-NTU turbidity sensor (Sea-Bird Scientific, Washington, USA) deployed in each site (Appendix A Figure S2.1). Sensors were programed to record three NTU measurements at 15 minute intervals from Swift Current and Baie de l'Eau during June-November 2020 and from North Harbour, during August-November 2020.

Season	Site	NTU	Stdev
Summer	North Harbour	No Data	No Data
	Swift Current	0.54	0.12
	Baie de l'Eau	0.21	0.16
Fall	North Harbour	0.14	0.063
	Swift Current	1.03	1.2
	Baie de l'Eau	0.077	0.024

Table 2.3: Confusion matrices for the validation data of the supervised image classification of each site (Figure 2.3A-F). Orthomosaics were created using a remotely piloted aircraft system (RPAS).

North Harbour Summer

Prediction	Deep water	Submerged eelgrass	Exposed macroalgae	Submerged macroalgae	Unvegetated
Deep water	32	1	0	0	0
Submerged eelgrass	0	18	0	4	0
Exposed macroalgae	0	0	30	0	0
Submerged macroalgae	0	1	0	9	11
Unvegetated	0	8	1	0	23

North Harbour Fall

Prediction	Deep water	Submerged eelgrass	Exposed macroalgae	Submerged macroalgae	Unvegetated
Deep water	31	0	0	3	0
Submerged eelgrass	0	26	0	1	1
Exposed macroalgae	0	0	29	0	2
Submerged macroalgae	0	6	0	12	2
Unvegetated	0	0	1	2	25

Swift Current Summer

Prediction	Deep water	Submerged eelgrass	Exposed eelgrass	Submerged macroalgae	Substrate
Deep water	22	5	0	0	0
Submerged eelgrass	4	16	0	0	5
Exposed eelgrass	0	0	20	2	0
Macroalgae	0	3	10	18	11
Unvegetated	0	4	0	9	18

Swift Current Fall

Prediction	Deep water	Submerged eelgrass	Exposed macroalgae	Submerged macroalgae	Unvegetated
Deep water	20	0	0	0	0
Submerged eelgrass	0	18	3	1	6
Exposed macroalgae	0	0	26	0	0
Submerged macroalgae	7	0	0	14	2
Unvegetated	0	13	1	2	22

Baie de l'Eau Summer

Prediction	Submerged eelgrass	Exposed macroalgae	Submerged macroalgae	Unvegetated
Submerged eelgrass	25	0	12	4
Exposed macroalgae	0	24	0	2
Submerged macroalgae	8	0	16	6
Unvegetated	0	6	3	14

Baie de l'Eau Fall

Prediction	Submerged eelgrass	Exposed macroalgae	Submerged macroalgae	Substrate	Sparse eelgrass
Submerged eelgrass	13	0	8	0	2
Exposed macroalgae	0	9	0	0	0
Submerged macroalgae	2	0	23	0	5
Unvegetated	0	0	0	3	3
Sparse eelgrass	0	0	1	28	2

Table 2.4: Count model coefficients for zero inflated poisson (ZIP) regression models relating eelgrass percent cover estimates to season, site, and location. Two models were conducted for each survey method, remotely piloted aircraft system (RPAS) and snorkel transect survey. Models were generated using a log link. Outside transect data were omitted for the snorkel model because all values of eelgrass were zero.

		RPAS		
Covariate	Estimate (%)	St. Error (%)	*P*-value	*95% CI*
Intercept	4.2	0.028	**<0.001**	[4.15, 4.26]
Summer	0.066	0.025	**0.009**	[0.016, 0.15]
North Harbour	-0.073	0.029	**0.01**	[-0.13, -0.017]
Swift Current	-0.59	0.034	**<0.001**	[-0.65, -0.52]
Inside	0.17	0.027	**<0.001**	[0.12, 0.23]
Outside	-0.60	0.042	**<0.001**	[-0.68, -0.52]
		Snorkel		
Covariate	Estimate (%)	St. Error (%)	*P*-value	*95% CI*
Intercept	4.05	0.029	**<0.001**	[3.99, 4.11]
Summer	0.0047	0.025	0.85	[-0.045, 0.055]
North Harbour	0.073	0.029	0.011	[0.016, 0.013]
Swift Current	-0.46	0.034	**<0.001**	[-0.53, -0.39]
Inside	0.48	0.027	**<0.001**	[0.43, 0.53]

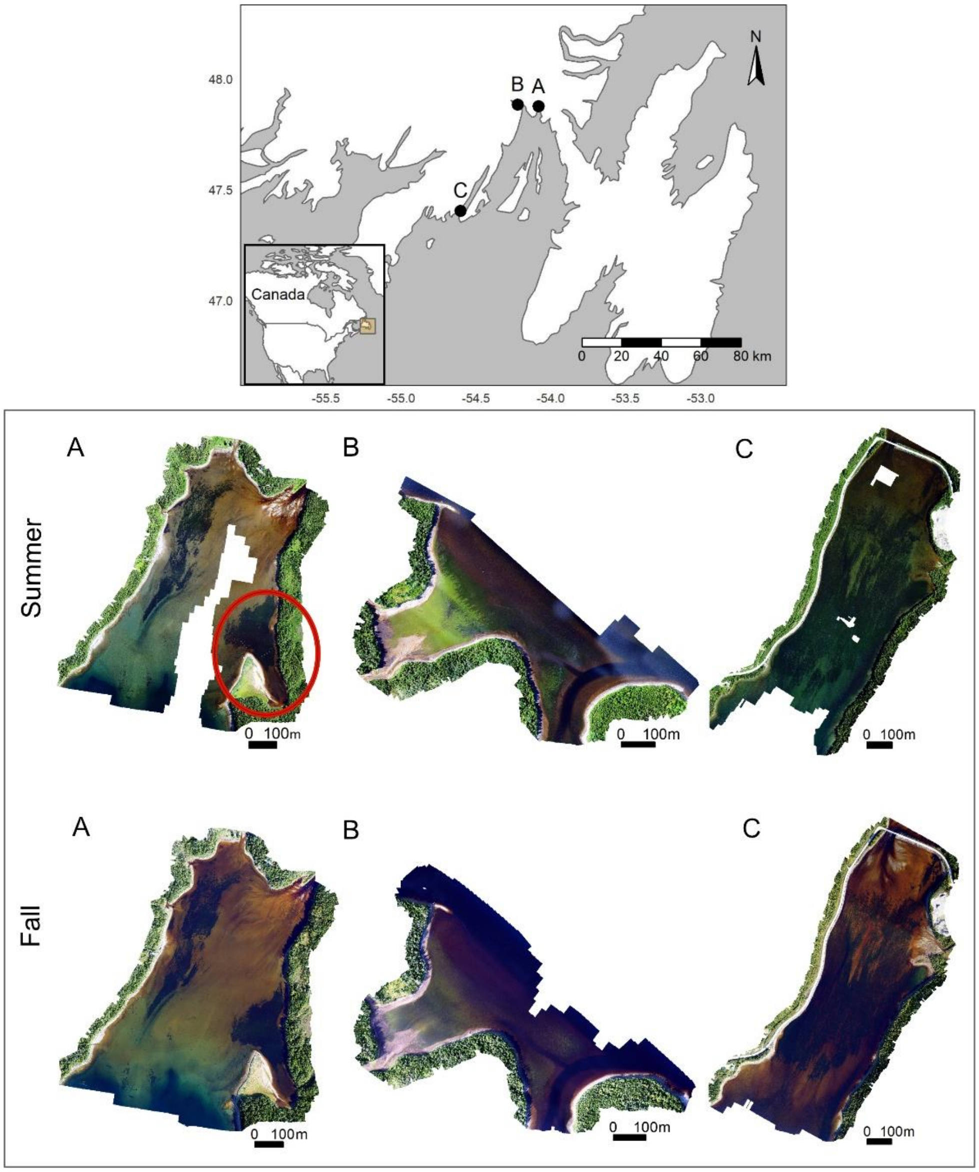

Figure 2.1: Map of survey locations (top) and seasonal orthomosaics of (A) North Harbour, (B) Swift Current, and (C) Baie de l'Eau, created using a remotely piloted aircraft system (RPAS) flown at 115 m altitude. Images were collected in the summer and fall of 2020. Red circle in (A) outlines subsite Caplin Cove. Map of survey location (top) was created using shapefiles from the R package *tmap* (Tennekes 2018) and from Natural Earth (2021) and using the WGS84 coordinate reference system.

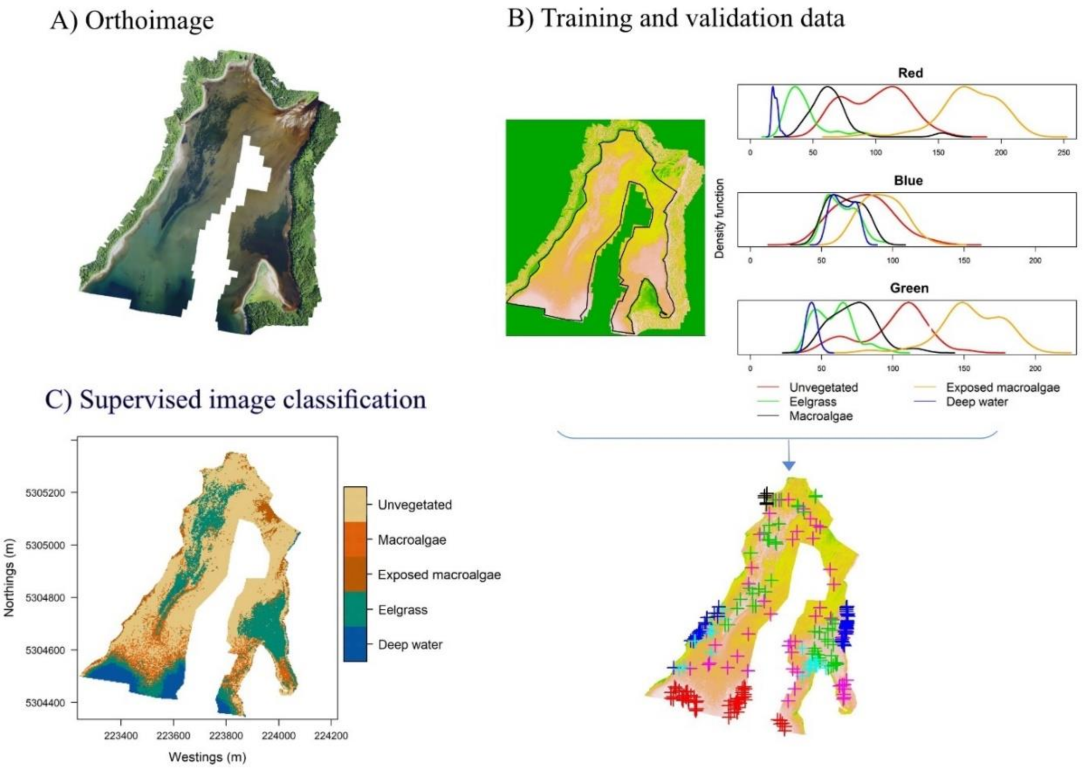

Figure 2.2: Workflow for random forest supervised image classification of remotely piloted aircraft system (RPAS) survey imagery. Workflow steps include A) collecting RPAS imagery and generating the orthoimage, B) masking land and creating training and validation data, C) using training data to conduct supervised image classification using random forest analysis to classify the orthoimage, and validate the model using validation data.

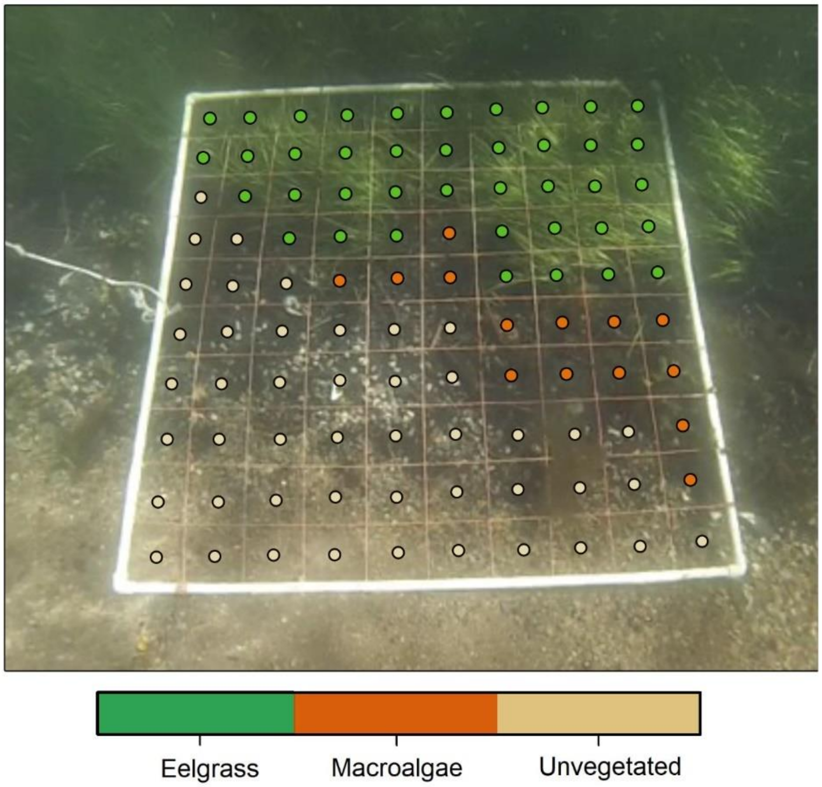

Figure 2.3: Image taken from the GoPro video of the 1 m × 1 m submerged quadrat for the quadrat altitude test. Quadrat was divided into a 0.1 m × 0.1 m grid. Coloured circles represent the habitat that each square was assigned via visual inspection.

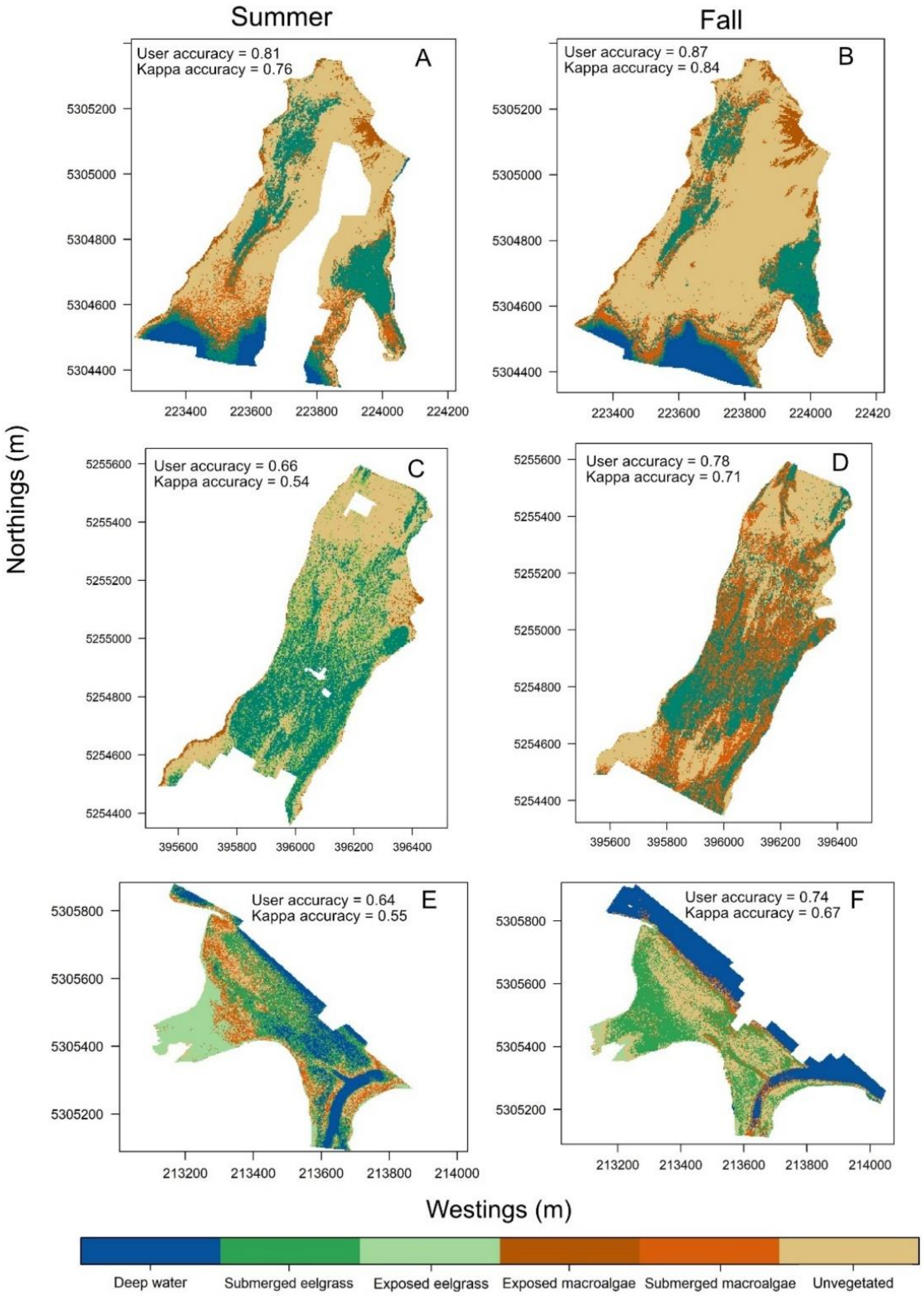

Figure 2.4: Random forest supervised image classification of North Harbour (A and B), Bay de l’Eau (C and D) and Swift Current (E and F). Surveys were conducted at 115 m altitude in the summer and the fall.

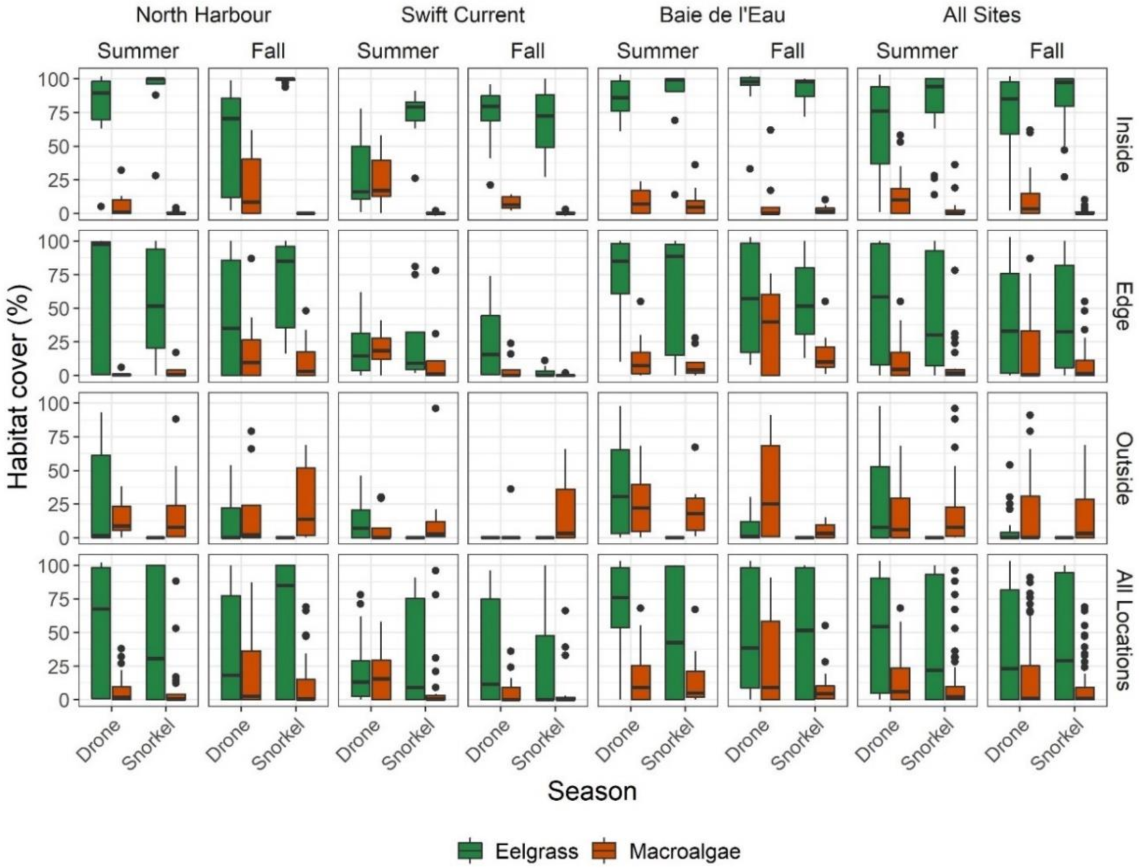

Figure 2.5: Boxplots comparing the percent habitat cover (%) of eelgrass (green) and macroalgae (orange) measured each season using a remotely piloted aircraft system (RPAS) at 115 m altitude versus the snorkel quadrat survey. Panels are broken down by survey site, season, and by location of the quadrats relative to the eelgrass meadow.

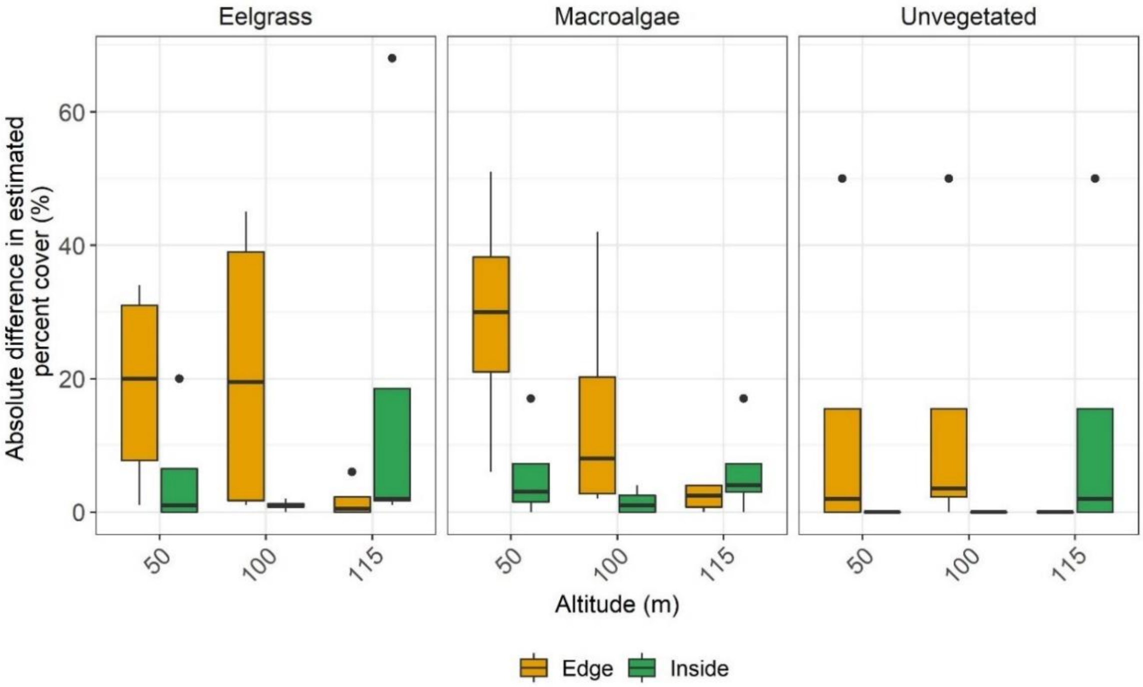

Figure 2.6: Relationship of increasing the remotely piloted aircraft system (RPAS) altitude on estimates of eelgrass, macroalgae, and unvegetated percent cover compared to snorkel transect estimates. Boxplots show the percent differences (absoulte values) in estimates between the two survey methods with increasing RPAS survey altitude, where $n_{quadrat/transect} = 4$. Black line represents the median, boxes represent the upper and lower quartiles, whiskers describe the range of the data, and black dots represent outliers. Yellow boxes show differences for transects at the edge of the meadows and green boxes show differences for transects inside the meadows.

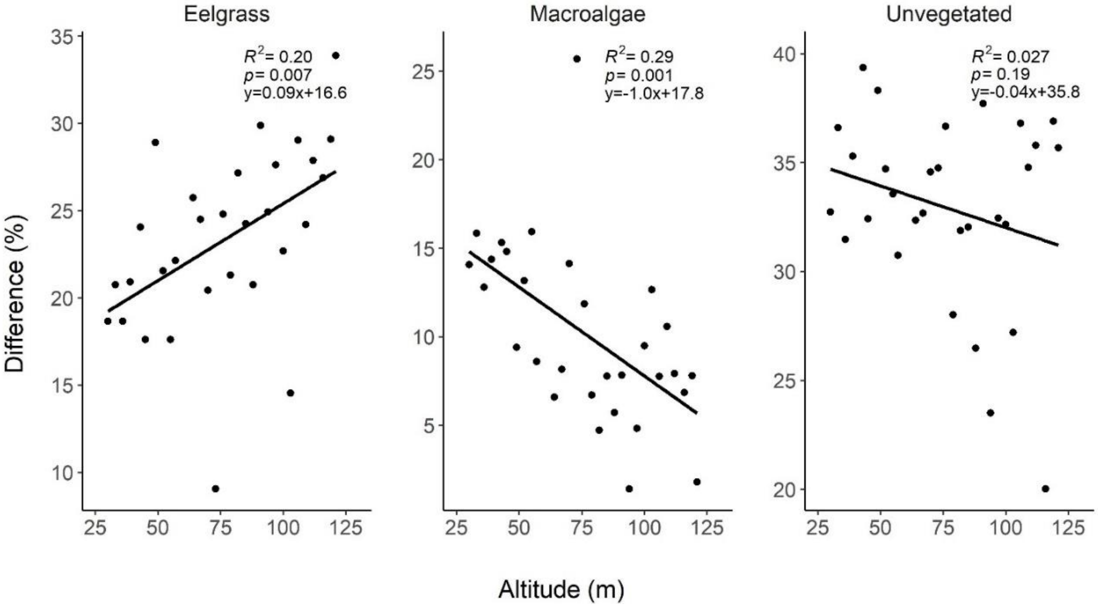

Figure 2.7: Relationship between increasing the remotely piloted aircraft system (RPAS) altitude and the absolute value differences in estimates of eelgrass, macroalgae, and unvegetated cover. Differences (%) on the y-axis were calculated as the absolute value of the difference between the habitat cover (%) measured using an RPAS and the percent habitat cover calculated from a GoPro underwater image of the same quadrat (Figure 2.3). Black dots represent estimates using RPAS images.

Chapter 3: Characterizing eelgrass meadow traits that promote fish taxonomic and life history diversity

3.1 Abstract

Seagrass meadows enhance faunal taxonomic diversity compared to unvegetated habitat. However, habitat traits and environmental conditions that enhance taxonomic diversity do not consistently increase life history diversity, implying there are mechanistic differences underpinning seagrass meadow effects on different components of diversity. This study sought to assess whether eelgrass (*Zostera marina*) meadows enhance both fish species richness (estimate of taxonomic diversity) and diversity in life history traits, and to identify habitat traits underpinning the relationships. Using a seine net survey (127 tows) across three eelgrass meadows located in Placentia Bay, Newfoundland and Labrador, Canada, I related taxonomic and life history trait (LHT) diversity to meadow traits and oceanographic variables. Results showed that variability in taxonomic and life history diversity was detected at the meadow scale (i.e., within meadow variability), but not at the bay scale (i.e., among meadow variability). Species richness and the probability of detecting LHT diversity was higher inside the meadow compared to outside. However, this study also shows that habitat traits underpinning fish diversity in eelgrass meadows vary depending on the diversity index. Both indices decreased with increasing depth, but LHT diversity followed a positive relationship with salinity whereas species richness followed a positive relationship with eelgrass percent cover. These findings indicate that eelgrass meadows promote taxonomic and life history diversity in fish communities.

Therefore, efforts to conserve eelgrass meadows could contribute to biodiversity conservation, and ultimately enhances ecosystem resilience to disturbances.

3.2 Introduction

Biodiversity bolsters community resilience against environmental perturbations (Duffy 2006; Palumbi et al. 2009). Biodiverse communities modify ecosystem functions through direct effects of individual species (e.g., sediment resuspension), interactions among species (e.g., predation), and through non-additive effects of species and their interactions (Chapin et al. 2000; Duffy et al. 2005; Duffy 2006). Furthermore, biodiverse communities are more resilient to environmental disturbances due to the differential ability of species to withstand and recover from disturbances (Hilborn et al. 2003; Capdevila et al. 2022) and because modifications to the community interaction network are likely to be smaller in more complex networks composed of species with ecological redundancies (i.e., species that provide similar ecosystem functions; Naeem 1998; Tylianakis and Morris 2017). As environmental perturbations continue to escalate due to climate change and other anthropogenic threats (Lotze et al. 2006; Halpern et al. 2008; Bindoff et al. 2019), describing the mechanisms driving species diversity within a community is important for knowing where to focus conservation efforts.

Habitat is a well-known driver of species community composition and biodiversity in the coastal zone (Gray 1997; Schein et al. 2012). Foundation species, such as seagrasses, provide structures that create habitats supporting diverse fish species assemblages (Heck and Thoman 1981; Cullen-Unsworth and Unsworth 2013). The relationship between seagrass and biodiversity has received considerable attention (Boström et al. 2006), particularly for indices of taxonomic diversity (e.g., species richness) and abundance (e.g. Hovel et al. 2002; Boström et al. 2006; Robinson et al.

2011; Cote et al. 2013; Jones et al. 2021). However, taxonomic diversity does not account for the effects of species on ecological redundancies, where different species may provide similar roles or may contribute proportionally more to ecosystem functioning (Halpern and Floeter 2008). As a result, there is increasing interest in examining the relationship between habitat and biodiversity by focusing on trait-based diversity indices that inform on species role in a community, rather than focusing on species entities alone (McGill et al. 2006; Mims et al. 2010; Wong and Dowd 2015; Wong and Kay 2019).

Life history classification provides a trait-based approach for examining the relationship between environmental drivers and species fitness and performance (Winemiller and Rose 1992; Tilman 2001; Petchey and Gaston 2006). Life history strategies are a suite of heritable traits, such as reproductive strategy and habitat use, that enable a species to cope with ecological perturbations. Species with different life history traits (e.g., growth rates, habitat use, feeding) differ in their distribution and dispersal ability, reproduction and abundance, and resource uses, resulting in numerous types of interactions with the ecosystem (Chapin et al. 1997, 2000). These interactions ultimately affect ecosystem functioning by modifying processes such as nutrient pathways and the rate of nutrient uptake or burial, interspecific competition, and physical alterations to the surrounding environment (Chapin et al. 2000; Duffy et al. 2005; Duffy 2006). For instance, nest digging and bottom feeding increase bioturbation and nutrient resuspension (Moore 2006). Because ecosystem functioning is complex and does not necessarily vary linearly according to species taxonomic composition, examinations of relationships between habitat complexity and fish taxonomic diversity versus life history diversity may yield divergent results (Duffy et al. 2005; Wong and Dowd 2015; Wong and Kay 2019). For instance, studies on fish (Wong and Kay 2019) and microbenthic invertebrates (Wong and Dowd 2015) observed higher taxonomic diversity inside eelgrass meadows compared to unvegetated habitat. In contrast, differences in functional diversity (defined as a combination of life history and trophic traits in their studies) across habitat types appeared unaffected by the different habitat types (Wong and Dowd 2015) or yield opposite trends (i.e., lower functional diversity in taller canopy; Wong and Kay 2019). Different relationships between habitat structure and taxonomic versus trait-based diversity indices suggest there are likely mechanistic differences between seagrass structural complexity and components of ecosystem functioning, including life history diversity.

Seagrass meadows vary in structural complexity, such as blade length and density. Faunal species assemblages and interactions may vary between meadows according to heterogeneity in these structural features (Boström et al. 2006; Jones et al. 2021). For instance, in Tanzania, fish abundance has been shown to increase in areas with taller seagrass canopy and more blades per shoot (Jones et al. 2021). Similarly, seagrass meadows vary in landscape complexity, where some meadows are patchy (homogenous areas of seagrass, a patch, interspersed with unvegetated or macroalgae areas, where seagrass patches can vary in size and configuration), others continuous, and others a hybrid (Hemminga and Duarte 2000b; Thistle et al. 2010). Meadow edges, the transition zones between seagrass patches and unvegetated habitat, provide corridors facilitating foraging (Renkawitz et al. 2011), while patches provide refuge from predation and enhance epifaunal settlement (Heck et al. 2003; Laurel et al. 2003a; Gorman et al. 2009), and as a results meadows with intermediate spatial complexity have been suggested to host higher fish densities (Thistle et al. 2010). However, the conditions maintaining relationships between habitat heterogeneity and biodiversity are idiosyncratic (Boström et al. 2006, 2011; Duffy 2006; Gillanders 2006) and depend on the scale at which biodiversity is analysed (i.e., alpha, vs. gamma diversity; Schneider et al. 2008; Whippo et al. 2018). Furthermore, variability in other environmental parameters including oceanographic parameters (e.g., temperature, salinity, dissolved oxygen) can have physiological implications on fauna, affecting local biodiversity and potentially confounding the detection of biodiversity responses to habitat characteristics (Ewers and Didham 2005). This variability is especially high in estuarine environments where seagrass meadows exist (Bulger et al. 1993; Thom et al. 2003b).

To better understand how seagrass meadows benefit fish diversity, this study relates eelgrass (*Zostera marina*) structural complexity and oceanographic parameters to fish species richness (estimate of taxonomic diversity) and life history trait (LHT) diversity. I explored this relationship at two spatial scales: the bay scale (i.e., gamma diversity) by comparing fish diversity among three meadows in Placentia Bay, Newfoundland, and the meadow scale (i.e., alpha diversity) by dividing each meadow according to the inside, edge, or outside of the meadow. This study focuses on *Zostera marina* (eelgrass) as it is the dominant seagrass species in eastern Canada (Murphy et al. 2021). Given that LHT are heritable traits that enable a species to cope with ecological perturbations, I hypothesized that eelgrass meadows would harbour a higher taxonomic and life history diversity compared to sediment habitat outside the meadow, where both diversity indices would be higher inside the meadows compared to the edge. However, relationships between meadows traits and fish diversity will vary depending on the index and spatial scale analysed.

3.3 Methods

3.3.1 Study design

Data were collected from three eelgrass meadows in Placentia Bay, Newfoundland: North Harbour (47°52.703'N, 54°4.971'W), Swift Current (47°52.878'N, 54°13.467'W), and Baie de l'Eau (47° 25.602'N, 54° 47.406'W) (Figure 3.1). I marked six transects per meadow ($n_{transect}$=18) using rebar embedded into the shoreline. Transect locations were selected such that, for each meadow, two transects intersected the middle, two intersected within 2 m from the edge, and two transects were located outside the meadow (Figure S2.1; same transects used in Chapter 2). Transect were also marked in areas that were conducive to seine net sampling (i.e., area to sort fish on shore and no large boulders that the net could snag on).

3.3.2 Assessing eelgrass meadow landscape metrics and structural traits

Meadow-scale landscape descriptors were calculated using the eelgrass maps created in Prystay et al. (2023, Chapter 2 of this thesis). I selected the maps that best represented each meadow according to my knowledge of the study sites and decreased the resolution to 30 × 30 cm to accommodate computer limitations during landscape analyses.

Landscape descriptors, including eelgrass coverage area, perimeter, area-perimeter ratio, and median minimum distance between patches were calculated using the *sf* (Pebesma 2018) and *landscapetools* (Sciaini et al. 2018) packages in R (v. 4.1.3; R Core Team, 2022). The eelgrass meadow in Swift Current extended beyond the area that was mapped and landscape descriptors were therefore only calculated for the area that was mapped.

Between September 30 to October 2, 2020, I assessed heterogeneity in structural traits within the meadows using snorkel quadrat surveys along the marked transects. Snorkel transect surveys were guided using a 50 m lead line marked every 10 m extending perpendicular to shore starting from the water's edge. A 1 m^2 quadrat divided into 10 × 10 cm grid cells was deposited every 10 m starting at the 20 m marker. Eelgrass percent cover was assessed according to the number of grid cells containing eelgrass shoots (Thomson et al. 2015). Three eelgrass shoots were then collected from the middle of each quadrat to measure morphological parameters. If eelgrass shoots were absent in the middle of the quadrat, they were collected from the next closest cell. This approach was used to avoid sampling bias. In the cases where eelgrass was altogether absent from the quadrat (e.g., outside transects or gaps between meadow patches), no eelgrass samples were collected. Plants were then rinsed in the lab, the rhizomes removed, and in the few cases when present, epiphytes were gently removed using a sharp scalpel (Jensen and Bell 2000). Blade length and width of the longest blade of each shoot were then measured before drying eelgrass shoots at 60°C for 48 hours and collecting blade dry mass (Thomson et al. 2015). This procedure was completed once per transect in each site.

3.3.3 Fish surveys

All fish surveys occurred between October 5-29, 2020. Timing of sampling was selected to coincide with date when eelgrass were at or near peak density and when fish biodiversity is known to be high and juvenile Atlantic cod (*Gadus morhua*) are settled in shallow water (Methven and Schneider 1998; Methven et al. 2001). For each site and transect, fish were sampled using a beach seine net (50 m long, 5 mm mesh size) deployed from the back of a boat and in alignment with the rebar transect marker. The seine net was manually pulled along the seafloor by two individuals standing onshore approximately 10 m apart, therefore surveying 500 m^2 per tow. This approach has been shown to capture 95% of the fish in the seine net tow trajectory (Gotceitas et al. 1997). Once onshore, fish were transferred into a cooler containing clean seawater. I identified individuals to the species level then measured the total length (TL) of each individual before releasing them in the same location they were captured. In the case where there were many individuals of the same species, I measured the total length of 20 individuals and counted the number of the remaining individuals. Once all fish were measured and identified, I collected oceanographic parameters relevant to fish physiology and that may affect species aggregation, namely temperature, salinity, and dissolved oxygen (DO), and depth. Water quality parameters were measured approximately 50 m from shore, in line with the transect marker, and recorded over 3 minutes at every 1 m depth, stopping approximately 10 cm above the seafloor. Temperature, salinity, and water depth were measured using an RBRconcerto³ sensor programmed to record every 0.1 seconds and DO was measured using a miniDOT USB oxygen logger programmed to record DO every 1 minute (lowest temporal resolution of the sensor). To increase statistical power, fish sampling procedures were repeated 6 to 9 times per transect for each site ($n_{tows} = 127$; Figure S3.1), while ensuring to evenly distribute sampling throughout the month and tide heights.

3.3.4 Statistical analyses

Life history diversity was determined by examining the variability in species morphological, behavioural, and reproductive traits. (Table 3.1). Traits were assigned to each species using fish lengths collected in the field and using information collected from Wroblewski et al. (2007), Scott and Scott (1988), and FishBase (www.fishbase.ca). In the few cases where data were unavailable in the three primary sources, I used other literature on the same species or a closely related species (i.e., blue runner *Caranx crysos*: Devine and Fisher, 2014 [migration and use of coastal zone], James, 1976 [estimate of egg size according to data from *Caranx georgianus*]; Greenland cod (*Gadus macrocephalus ogac*): Andersen, Nielsen and Smidt, 1994 [egg size]) (see Table S3.1 in Appendix B for trait classification). These traits were used to calculate life history diversity at the transect level, following similar methods to those outlined in Wong et al. (2015). The methods for calculating life history diversity first involved converting the trait matrix into a binomial matrix, where “1” meant the species exhibited the trait, and “0” meant the species did not exhibit the trait (see Appendix B Table S3.2 for matrix). Life history traits (LHT) diversity was then calculated using the Rao Quadratic Entropy Index (Rao 1982),

$$LHT = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{i,j} p_i p_j,$$

where $d_{i,j}$ is the dissimilarity between species i and j in each transect measured using Euclidean distance between traits and p is species proportional abundance. Hence, this approach accounts for species abundance and dissimilarity among traits within each transect, both of which are important for characterising species interactions with the habitat. Instances where species did not share traits in common, LHT diversity index is equivalent to the Gini-Simpson index (Dray et al. 2023). The final LHT diversity index used in subsequent analyses consisted of the mean of the LHT diversity indices calculated for each trait. All statistical analyses were conducted using R (R Core Team 2022), where species dissimilarities were calculated using the *vegan* package (Oksanen et al. 2022) and LHT diversity was calculated using the *Ade4* package (Dray and Dufour 2007).

The resulting LHT diversity across seine net tows was zero-inflated and continuous. Therefore, I evaluated trends in LHT diversity using a zero-inflated generalized linear mixed effect model (GLMM) with a gamma distribution. First, I tested whether LHT diversity differed between sites and locations in the meadows (i.e., inside, edge, outside), where in both the conditional and the zero inflated model, site and location were fixed effects, and transect ID was set as a random effect to account for dependencies among seine net tows conducted along the same transect. Differences among sites were inspected using the Bonferroni corrected 95% confidence intervals of the fixed effects (Midway et al. 2020). I then applied a third model to identify habitat traits driving variability in LHT diversity. Although I measured landscape metrics for each site, I could not include them as covariates given that they were equivalent to categorical site covariates. Therefore, in this model, eelgrass percent cover, sediment bulk density (correlated with sediment organic carbon and nitrogen content (p-value < 0.001; $r_s = -0.81$ for both cases); see data collection and processing in Chapter 4) and water quality parameters (averaged across depths for each tow) including temperature, DO, salinity, and water depth were included as fixed effects, and again transect ID was included as a random effect. Eelgrass blade width and mass were correlated with blade length and therefore were excluded as covariates in the models. Given that there was no eelgrass in the outside transect and a blade length of zero would be misleading, this third model was repeated twice. The first iteration included outside transects and only eelgrass percent cover was evaluated as a descriptive eelgrass trait. The second iteration excluded outside transects and eelgrass blade length was included as an additional eelgrass trait. For both iterations, model selection was conducted using a stepwise model selection and selecting the most parsimonious model according to the lowest AIC score.

Next, species richness was calculated according to the number of species present in each seine net tow. I used GLMMs with a Poisson distribution to assess whether species richness differed between the three meadows and between locations within the meadow. I evaluated relationships between species richness and eelgrass structural complexity following the same two-model approach outlined above. As in the previous models, transect ID was included as random effect to account for dependencies and models were simplified to the most parsimonious version according to the lowest AIC score. All statistical models were created using the *glmmTMB* package (Brooks et al. 2017) and the residuals were inspected for model fit.

Lastly, if species richness or LHT diversity varied significantly among sites or locations, I examined differences in community composition (i.e., beta diversity) at that spatial scale. First, I quantified the species compositional dissimilarity between tows using the Bray-Curtis dissimilarity index via the *vegdist* function in the *vegan* package (Oksanen et al. 2022). I selected the Bray-Curtis index because it accounts for species presence and abundance in the community. Variability in community dissimilarity among locations was then compared using the *betadisper* function in the *vegan* package followed by a Tukey's multiple comparison analysis. The *betadisper* function conducts a PERMANOVA to test for homogeneity of variances across groups (in this case locations) and the dissimilarity indices were square root transformed to reduced the influence of skewed samples (Cote et al. 2013; Oksanen et al. 2022). Finally, I identified the species driving variability in community composition by using the *simper* function in the *vegan* package. Doing so calculates the contribution of each species to the Bray-Curtis dissimilarity index.

3.4 Results

3.4.1 Species

A total of 24 species were detected among the three eelgrass meadows (Table 3.2). Fish lengths ranged between 10-275 mm TL, and included resident species (e.g., stickleback [*Gasterosteus* sp.], flounder [*Pleuronectes putnami*]) that use eelgrass habitats year round, as well as transient species (e.g., capelin [*Mallotus villosus*], sandlance [*Ammodytes americanus*], rainbow smelt [*Osmerus mordax*]) that use eelgrass habitats only for foraging and spawning, and anadromous and ocean migrant species that use eelgrass as a nursery habitat before migrating offshore (e.g., brown trout [*Salmo trutta*], Atlantic salmon parr [*Salmo salar*], Atlantic cod [*Gadus morhua*]) (Appendix B Table S3.1).

3.4.2 Variability among sites

The three eelgrass meadows varied in landscape complexity, where Baie de l’Eau covered an area almost four-fold larger than North Harbour (Table 3.3). Swift Current covered the largest area of the three meadows, however, only a portion of the meadow was mapped. Baie de l’Eau also had the greatest area-perimeter ratio (1.13 m) and median distance between patches (0.85 m), followed by North Harbour (1.09 m, 0.67 m), with Swift Current being the least patchy meadow (0.72 m, 0.6 m). Furthermore, the meadows varied in structural complexity, where Swift Current had substantially longer and wider eelgrass blades than the other two sites yet was on average at least 10% sparser due to more space between individual shoots. North Harbour contained the highest species richness and LHT diversity compared to the other two sites and was the most likely to support a more LHT diverse population (Figure 3.2). Regardless of this apparent variability among the three meadows, neither species richness nor LHT diversity varied significantly among the three sites (Figure 3.2B, C).

3.4.3 Variability among locations

Although LHT diversity was zero-inflated because tows often captured individuals that belonged to the same species, LHT diversity was >0 in 68% of the tows.

The probability of detecting zero LHT diversity increased with increasing distance from the meadow and this probability was significantly higher outside the meadow compared to inside (Figure 3.3C). However, when >0, LHT diversity did not vary significantly among locations within each site (Figure 3.3A, B). Instead, variability in LHT diversity was related to salinity and depth (Table 3.4). Specifically, when >0, LHT diversity increased with salinity (Figure 3.4A). Within the meadow (i.e., examining inside and edge only), LHT diversity continued to follow a positive relationship with salinity, but decreased in deeper portions of the meadow (Figure 3.4B). These patterns were attributed to species movement life history traits (i.e., resident, ocean migratory, or anadromy) (Figure 3.5).

Species richness varied according to location in the meadow (Figure 3.3A, B). The maximum number of species caught in one 500 m^2 tow was only six, where on average inside transect tows detected 3.33 ± 1.4 species compared to 2.13 ± 1.2 species in the edge transects and 1.22 ± 1.2 species in the outside transects. Correspondingly, species richness was statistically higher inside the meadow compared to outside (Figure 3.3B). Species richness was also higher in the edge of the meadow compared to outside and on average lower compared to inside the meadows, but these differences were not statistically significant. Variability in species richness was best explained by eelgrass percent cover and water depth (Table 3.4). Specifically, species richness followed a positive correlation with eelgrass percent cover, which was highest inside the meadow (Figure 3.4C), but a negative correlation with water depth (Figure 3.4D). These trends remained consistent even when examining species richness within the meadow only, implying that species richness was unaffected by eelgrass blade length and blade width. The relationship between species richness and depth was not explained by oceanographic parameters nor changes in eelgrass percent cover or blade length, as none of these explanatory variables were correlated with depth.

Species community composition differed by location (PERMANOVA: $F_{2,110}$ = 7.41, p-value = 0.002) and was least variable inside the meadow compared to the edge and outside (Figure 3.6A,B; TukeyHSD: inside vs. edge p-value = 0.007 and inside vs. outside p-value = 0.002). In contrast, variability in species composition did not statistically differ between the edge and outside the meadow. Furthermore, >75% of the variability in species composition among locations were driven by six species, namely fourspine stickleback, threespine stickleback, Atlantic herring, rainbow smelt, and Atlantic silverside. However, approximately half of the variability was driven by variable occurrences of fourspine (32% inside vs. edge; 34% outside vs. edge; 35% inside vs. outside) and threespine stickleback (19.7% inside vs. edge; 29.8% outside vs. edge; 17.5% inside vs. outside) (Figure 3.6C). Of the six species accounting for most of the variability in species community composition among locations, five are schooling species and together account for 69-79% of the variability.

3.5 Discussion

By examining fish community diversity inside, at the edge and outside eelgrass meadows, this study shows that eelgrass meadows enhance both fish life history and taxonomic diversity. Specifically, I found that taxonomic diversity was highest inside the meadow and lowest outside the meadow, and that life history diversity was more likely to be null outside the meadows than inside and at the edge. This variability was predominantly driven by varying occurrences of schooling species, particularly resident threespine and fourspine stickleback. Furthermore, this study showed that the habitat traits underpinning fish diversity in eelgrass meadows vary depending on the diversity index used. Previous studies that have compared taxonomic diversity and other trait-based diversity indices such as functional diversity, generally defined functional diversity according to food acquisition and nutrient transfer (Villeger et al. 2010; Wong and Kay 2019). However, despite differences in the measure of trait-based diversity, findings from the current study coincide with previous studies showing partial agreement between trait-based and taxonomic diversity indices, highlighting the importance of considering multiple facets of diversity when assessing ecosystem biodiversity (Villeger et al. 2010; Wong and Dowd 2015; Wong and Kay 2019).

Eelgrass meadows are among the most productive marine ecosystems because they trap and retain organic matter generated from terrestrial runoff and tidal cycles, and their blades provide surface for epiphytes to grow (Hemminga and Duarte 2000a). This productivity enables eelgrass meadows to support more diverse fish communities by promoting foraging within meadows while providing structural shelter (Gorman et al. 2009; Renkawitz et al. 2011). However, predation risk is higher outside and at the edges compared to inside meadows (Heck and Thoman 1981; Laurel et al. 2003a; Gorman et al. 2009). Therefore, the observed distribution in species diversity is likely a consequence of forage-risk-trade-off (Eklöv and Halvarsson 2000; Hammerschlag et al. 2010). Smaller fish use eelgrass as refuge and for feeding on prey that consume epiphytes and other organic matter retained by eelgrass, while larger fish use the outside and edges of the meadow to forage for smaller fish. Predation interactions likely explain the higher variability in community composition at the edge and outside the meadow compared to inside in the current study. Most of the species underpinning the observed variability in community composition were species that school – a predator avoidance behaviour that is useful when there is limited refuge. Similarly, I also observed that larger fishes (e.g., Atlantic cod, Atlantic salmon) were more commonly caught outside the meadows while smaller fishes (e.g., threespine stickleback, silverside) were more commonly caught inside meadows. Although this would explain why species richness and the probability of detecting LHT diversity increased inside the meadow, LHT diversity (i.e., tows that sampled more than one species with different life history traits) did not vary spatially. Instead, this lack of spatial variation may be due to species with shared life history traits using similar habitats, causing them to aggregate spatially.

Numerous studies have related species spatial aggregation within eelgrass systems to habitat traits (Bell and Westoby 1986; Boström et al. 2006; Wong and Kay 2019; Jones et al. 2021). Here, variability in fish LHT diversity was best described by salinity and depth, whereas variability in species richness was best described by eelgrass percent cover and depth. Hence, depth was the only habitat trait that affected both species richness and LHT diversity in this study, both following a negative relationship. One reason could be that predation rates, which have been shown to increase with depth in a nearby eelgrass system, may be causing small fish to aggregate in shallow regions as an antipredation mechanism (Linehan et al. 2001). A second reason could be that depth-related oceanographic parameters, such as temperature and salinity, are influencing species abundance and diversity (Wong and Kay 2019; Jones et al. 2021). Temperature and salinity are generally correlated with depth; however, this was not the case in my study. While this lack of correlation may be because oceanographic variables were depth-integrated averages and depth was calculated as a maximum for each transect, it may also reflect the high variability typical of estuarine environments with high tidal, freshwater, and wind forces. Alternatively, greater species diversity associated with shallower depths is more likely to reflect the fact that the deeper sites in this study were located outside eelgrass meadows.

LHT diversity also increased in more saline environments, which was likely due to species physiological preferences (Bulger et al. 1993; Martino and Able 2003). Salinity tolerances and osmoregulation requirements influence energy allocation causing a trade-off between species movement, development (i.e., growth, reproduction), and habitat selection (Wendelaar Bonga 1997; Bœuf and Payan 2001; Mackenzie et al. 2007). Hence, fish may alter their behaviours to maintain homeostasis under stressful conditions, such as salinity extremes in estuarine environments. Coincidingly, laboratory-based and field-based studies have attributed fish distribution to be driven in part by environmental salinity and species osmoregulatory abilities (Serafy et al. 1997; Santos et al. 2018). Median salinity in my study system ranged between 6 and 31 psu, a high variability typical of estuarine environments. Euryhaline species including anadromous species or estuarine resident species, such as sticklebacks, can tolerate larger variation in salinity (Külts 2015). However, stenohaline species with affinities for higher salinity water, such as marine migrant species (e.g., Atlantic cod, white hake) and some coastal resident species (e.g., shorthorn sculpin, cunner), cannot reside in eelgrass meadows if the salinity is too low. These tolerance differences suggest the positive relationship between diversity and salinity could be caused by the movement of stenohaline species in eelgrass meadows from adjacent habitats with high tide. Examining fish migration life-history traits alone could not explain this hypothesis likely because fish migration traits did not fully account for species physiological preferences. Alternatively, salinity may influence fish abundance and distribution by affecting meadow structure (Santos et al. 2011, 2018), however, there was no apparent relationship between salinity and eelgrass cover or blade length in the current study.

Understanding the relationship between habitat structure and biodiversity depends on the scale at which habitats traits are analysed, how diversity is defined, and the scale at which species traits are analysed (i.e., individual vs. population vs. species levels) (Schneider et al. 2008; Wong and Carmona 2021). In this study, variability in species diversity was apparent at the meadow scale (i.e., location within meadows) but not at the bay scale (i.e., among meadows), possibly because habitat quality and connectivity to sites was similar among the three meadows at the bay scale (Duffy 2006; Cote et al. 2013). For instance, in contrast to my study, where fish diversity could not be related to carbon and nitrogen content (correlated to sediment bulk density), Unsworth et al. (2008) observed a relationship between sedimentary organic carbon content and fish abundance presumably due to the supply of organic carbon out-welling from adjacent mangrove habitats. Furthermore, my study defined diversity according to taxonomic richness and LHT diversity which was calculated according to traits defined at the species level. In doing so, I revealed that different habitat characteristics drove patterns in diversity for both indices. However, species also exhibit ontogenetic niche shifts, where traits defined according to the species scale may not best describe all life stages (Wong and Carmona 2021). For instance, it has been well documented that Atlantic cod use eelgrass habitat differently in their early life history (Lomond et al. 1998; Laurel et al. 2003a; Gorman et al. 2009; Renkawitz et al. 2011). Age 0 Atlantic cod, which feed on benthic prey, use eelgrass meadows as refuge from predators and are therefore more likely to use the inside and edges of meadows. In contrast, age 1 individuals, which transitioned to feed on smaller fish, use eelgrass to forage and are therefore more likely to use the outside and edges of the meadow. In recognition of such intraspecific variability in life histories, I attempted to repeat my assessment of LHT diversity where I divided fish species according to size and re-assigned life history traits accordingly. However, this process revealed that limited knowledge of fish behaviour and life history in these systems rendered adjusting classifications beyond the species levels challenging and uncertain. For instance, while Atlantic cod behaviour in eelgrass meadows has been relatively well-studied (Laurel et al. 2003a, 2003b, 2004; Ryan et al. 2012), knowledge about other species life history traits, such as white hake, is currently limited. For this reason, my study could only present results using LHT diversity traits defined at the species level. More work on understanding fish behaviour at various life stages in necessary if we are to fully understand the underlying ecological processes that enhance life history diversity.

While beach seine net surveys are effective non-destructive method for sampling fish communities, there are also limitations (Gotceitas et al. 1997; Nagelkerken et al.

2001; Guest et al. 2003; Unsworth et al. 2008; Cote et al. 2013). I could not control for cardinal direction because the coastline was non-linear and the transects had to be perpendicular to shore for sampling. This would result in varying light exposure among transects, which may affect eelgrass growth throughout the meadow and fish distribution (e.g., more direct sun exposure could increase temperature). Nevertheless, I did not observe a relationship between eelgrass blade length and depth (which would be correlated to light exposure), neither did I observe a relationship between biodiversity and temperature. Second, beach seine nets may be less effective at capturing fast-moving species and the substrate over which the seine net is pulled may affect sampling efficiency. For instance, there may be more opportunities for fish to escape outside the meadow if the substrate is rockier or in longer meadows (Nagelkerken et al. 2001). Attempts to compliment beach seine net tows with baited minnow traps were ceased early in the study as the traps lead to high densities of green crab that consumed the other captured fish. Yet, it is also worth noting that seine nets have been shown to yield better estimates of species proportional composition compared to trapping and trawling methods (Guest et al. 2003), and a study coupling seine net tows in eelgrass meadows with underwater surveys has shown that less than 5% of fish enclosed in the net escape (Gotceias et al. 1997; conducted in Newfoundland). The outside transects in my study were generally flat and therefore escapement was presumably low. Nevertheless, in future studies, this uncertainty could be addressed by coupling seine net surveys with other non-invasive survey methods, such as environmental DNA (He et al. 2022).

3.5.1 Conclusions

Warming waters are driving poleward shifts in species distributions (Perry et al. 2005; Pinsky et al. 2020). Being located on the south coast of Newfoundland, changes in fish community composition is already apparent in Placentia Bay. For instance, my study captured a juvenile blue runner in North Harbour, which is a tropical species that was first detected in Placentia Bay in 2013 (Devine and Fisher 2014). As shifts in species distribution become more prominent, we can expect shifts in local fish communities, altering taxonomic and life history diversity. These shifts in biodiversity may modify overall ecosystem functioning and therefore the provision of ecosystem services (e.g., recruitment of economically valuable species). This indicates a need to better understand and conserve the mechanisms relating coastal habitats to biodiversity to ensure that ecosystem service provision is maintained despite diversity modifications.

Conservation decisions often rely on indicators to suggest where to focus management efforts and how to plan management actions (e.g., transplanted patch size and configuration during restoration; Gagnon et al. 2023). Case studies used to determine indicators relating habitat to biodiversity have dominantly focused on taxonomic diversity indices that are not necessarily related to ecosystem functioning (Palumbi et al. 2009; Wong and Kay 2019). My study contributes to the growing body of evidence showing that the relationship between habitat and biodiversity depends on the diversity index used (Villeger et al. 2010; Cullain et al. 2018b; Wong and Kay 2019; Murphy et al. 2021; Wong and Carmona 2021). While eelgrass meadows increased both LHT diversity and species richness, this trend was only apparent at the meadow scale and habitat traits underpinning eelgrass function as a fish habitat varied depending on the index used. Nevertheless, this study also shows that eelgrass meadows promote taxonomic and life history diversity in fish communities, indicating efforts to conserve eelgrass meadows could contribute to biodiversity conservation, which ultimately enhances ecosystem resilience to disturbances.

Table 3.1: Traits used to characterise diversity of fish life history occurring in three eelgrass meadows in Placentia Bay, Newfoundland.

Trait	Categories	Description
Size	Small	Total length field measurements. Individuals ≤ 85 mm
	Medium	Total length field measurements. Individuals >85 mm but < 133 mm
	Large	Total length field measurements. Individuals ≥ 133 mm
Water column habitat	Demersal	Predominantly the sediment
	Benthopelagic	Predominantly on sediment surface
	Pelagic	Predominantly in the water column
Body shape	Ribbon	Long, eel-like shape
	Fusiform	Torpedo-shaped, slightly longer than wide
	Flat	Rounded laterally compressed body, flat on one side
	Elongated	Long and narrow body
	Compressiform	Deeper body than it is long
Behaviour	Schooling	Swims in school with other individuals of the same species
Reproductive behaviour	Parental care	Guard eggs post-fertilization
Use of eelgrass habitat	All life	Reside in eelgrass habitat year-round
	Refuge	Use the eelgrass habitat as shelter during development before migrating offshore
	Foraging	Forage in eelgrass meadows then move on to other habitats
Migration	Resident	Lives in seagrass habitat year-round
	Anadromous	Land-sea migration. Pass through seagrass meadows during spawning or return migration
	Oceanic migrant	Migrates from the ocean to seagrass habitats either to feed or to spawn
Egg type	Demersal	Eggs are deposited and sink to the seafloor
	Pelagic	Eggs are deposited into the water column and rely on physical forces (e.g., wind, currents) to transport eggs
Egg size	Small	Diameter ≤ 0.1 mm
	Medium	Diameter >0.1 mm to < 1.6 mm
	Large	Diameter ≥ 1.6 mm

Table 3.2: List of species captured from three eelgrass meadows in Placentia Bay, their total length (TL) reported as the mean ± the standard deviation, and the abundance of individuals captured from each species over the total sampling period.

Common name	**Scientific name**	**TL (mm)**	**Abundance**
Atlantic cod	*Gadus morhua*	149 ± 39	5
Atlantic herring	*Clupea harengus*	66 ± 8	148
Atlantic salmon parr	*Salmo salar*	124 ± 13	2
Atlantic Silversides	*Menidia menidia*	62 ± 17	91
Blackspotted stickleback	*Gasterosteus wheatlandi*	43 ± 5	12
Blue runner	*Caranx crysos*	218	1
Brook trout	*Salvelinus fontinalis*	202 ± 54	2
Brown trout	*Salmo trutta*	239 ± 29	2
Capelin	*Mallotus villosus*	55 ± 13	4
Cunner	*Tautogolabrus adspersus*	35 ± 9	7
Fourspine stickleback	*Apeltes quadracus*	47 ± 8	1683
Greenland cod	*Gadus macrocephalus ogac*	131 ± 47	8
Grubby sculpin	*Myoxocephalus aenaeus*	102 ± 21	41
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	108	1
Lumpfish	*Cyclopterus lumpus*	20	1
Rainbow smelt	*Osmerus mordax*	153 ± 56	285
Rock gunnel	*Pholis gunnellus*	100 ± 4	3
Sand lance	*Ammodytes americanus*	147 ± 32	19
Shorthorn sculpin	*Myoxocephalus scorpius*	113 ± 12	14
Smooth Flounder	*Pleuronectes putnami*	98	1
Threespine stickleback	*Gasterosteus aculeatus*	46 ± 16	1653
Tomcod	*Microgadus tomcod*	275	1
White hake	*Urophycis tenuis*	144 ± 48	6
Winter flounder	*Pseudopleuronectes americanus*	129 ± 40	15

Table 3.3: Landscape-scale (meadow) and structural (eelgrass) complexity of eelgrass bed and oceanographic characteristics for North Harbour (NH), Baie de l'Eau (BL), and Swift Current (SC). All data are presented as mean ± standard deviation, except for area:perimeter ratio and distance between patches which are presented as the median due to the wide spread in the data. No area is provided for Swift Current since only a portion of the meadow was mapped.

Site	Meadow				Eelgrass			Water quality				Sediment
	Area (m^2)	Perimeter (m)	Area:perimeter	Distance between patches (m)	Blade length (mm)	Blade width (mm)	Cover (%)	Temp. (°C)	Salinity (psu)	DO (mg L^{-1})	Depth (m)	Sediment bulk density (g cm^{-3})
NH	65445	60278	1.086	0.67	379±98	2.8±0.2	45±35	12.6±1.9	25.4±5.0	10.4±0.6	1.3±0.5	1.3±0.3
BL	255147	224905	1.134	0.85	331±134	2.2±0.5	47±41	13.1±1.3	28.3±1.5	10.3±0.8	1.2±0.5	1.3±0.4
SC	NA	NA	0.722	0.60	401±112	3.2±0.7	30±32	12.6±1.8	24.7±4.3	10.0±0.5	1.7±0.7	0.75±0.4

Table 3.4: Generalized linear mixed effect models comparing life history trait diversity and species richness to eelgrass cover and environmental parameters according to the most parsimonious model. Statistically significant covariates are in bold.

Response	**Transects included**	**Model**	**Covariate**	**df**	**Estimate**	**SE**	**Z value**	**p-value**
Life history trait diversity	In, edge, out	Conditional	Salinity	102	0.032	0.015	2.11	**0.035**
		Zero inflation	Eelgrass cover		-2.11	0.74	-2.86	**0.004**
			Salinity		0.15	0.084	1.82	0.069
			Depth		0.88	0.46	1.90	0.057*
	In, edge	Conditional	Salinity	72	0.047	0.015	3.09	**0.002**
			Depth		-0.34	0.15	-2.25	**0.024**
		Zero inflation	Depth		2.7	0.79	3.39	**<0.001**
Species richness	In, edge, out	Conditional	Eelgrass cover	125	0.85	0.18	4.67	**<0.0001**
			Depth		-0.27	0.12	-2.22	**0.026**
	In, edge	Conditional	Eelgrass cover	77	0.81	0.27	3.00	**0.0027**
			Depth		-0.33	0.15	-2.17	**0.030**

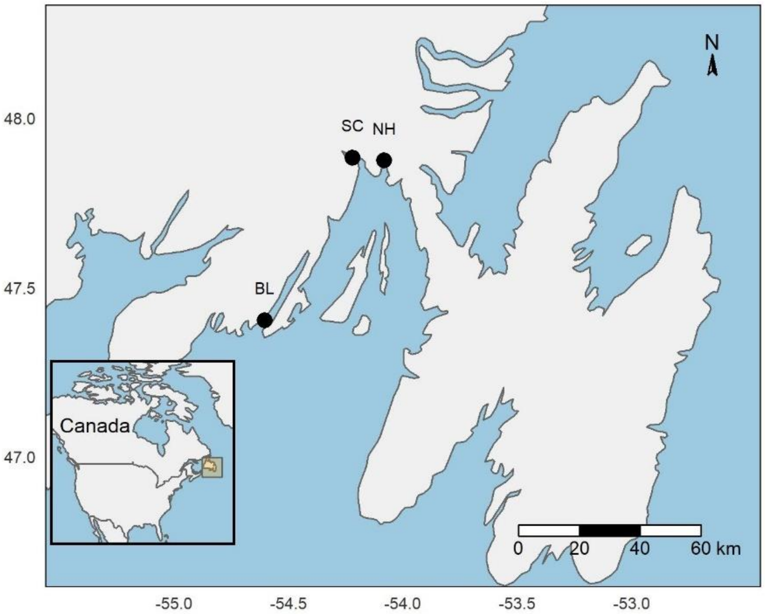

Figure 3.1: Map of study sites showing North Harbour (NH), Swift Current (SC), and Baie de l’Eau (BL). Figure was modified from Chapter 2.

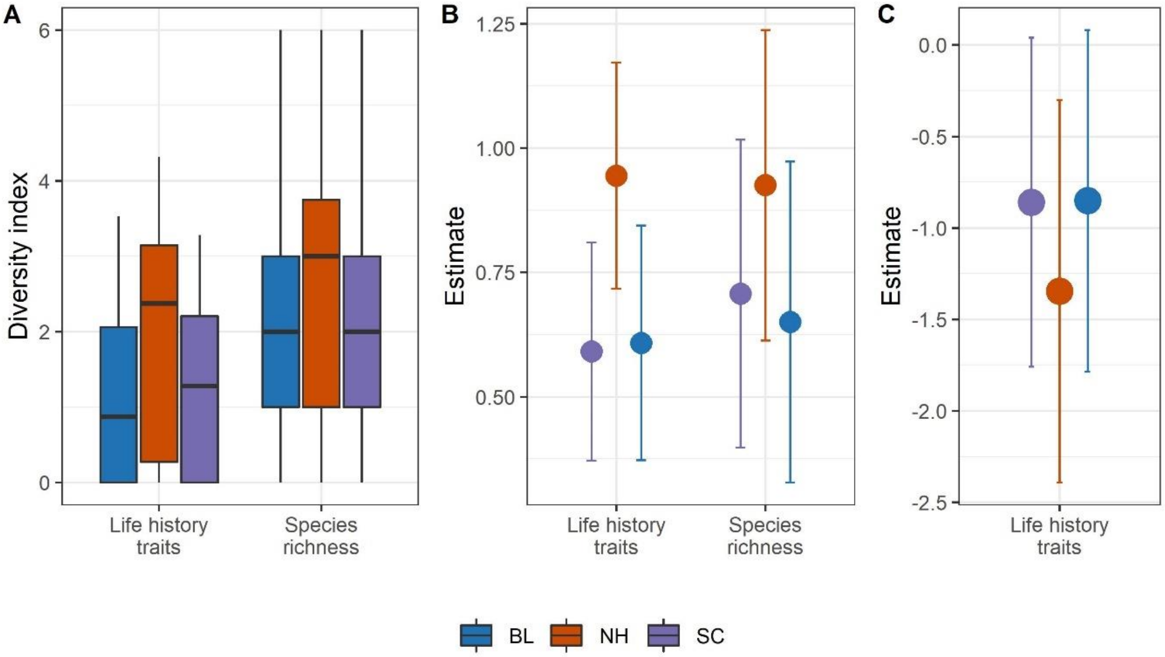

Figure 3.2: Boxplots showing spread in life history trait (LHT) diversity and species richness across the three eelgrass meadows (Baie de l'Eau (BL), North Harbour (NH), and Swift Current (SC)) (A), and Bonferroni corrected 95% confidence intervals of the site fixed effect estimate for species richness and the LHT conditional model (B) and the LHT zero inflation model showing the probability of detecting zero LHT diversity (i.e., lower estimate signifies lower probability of zero LHT diversity) (C). Fish were sampled using a seine net survey sampling 500 m^2 per tow.

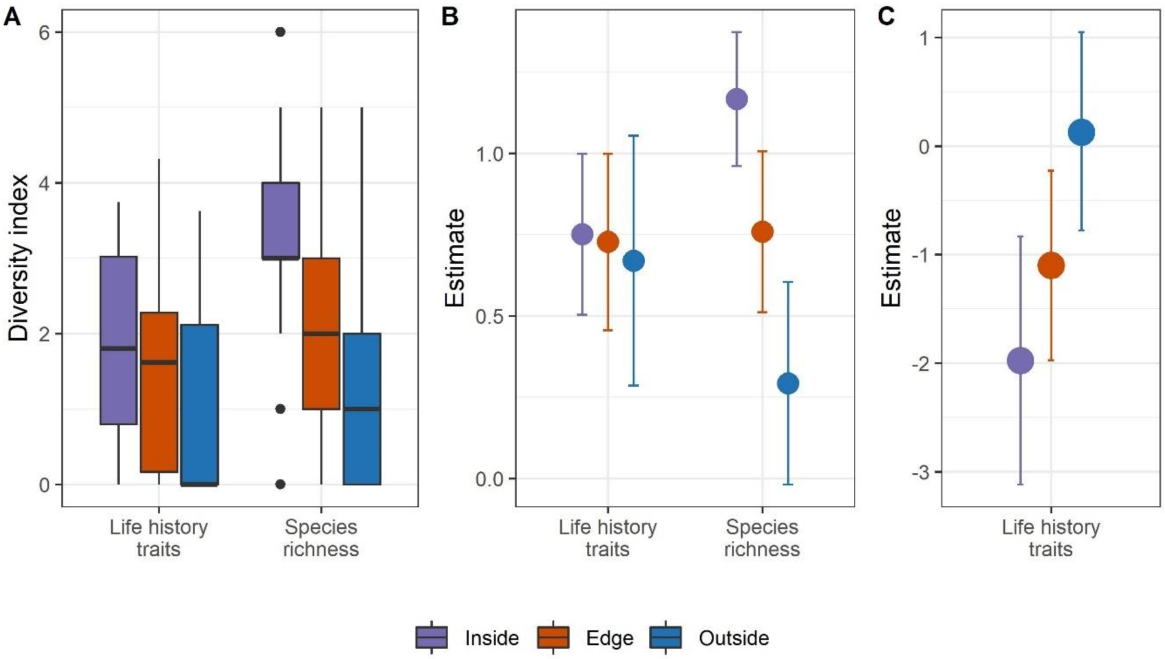

Figure 3.3: Boxplots showing spread in life history trait (LHT) diversity and species richness across the three locations relative to the eelgrass meadows (A), and Bonferroni corrected 95% confidence intervals of the location fixed effect estimate for species richness and the LHT diversity conditional model (B) and the LHT diversity zero inflation model showing the probability of detecting zero LHT diversity (i.e., lower estimate signifies lower probability of zero LHT diversity) (C). Fish were sampled using a seine net survey sampling 500 m^2 per tow.

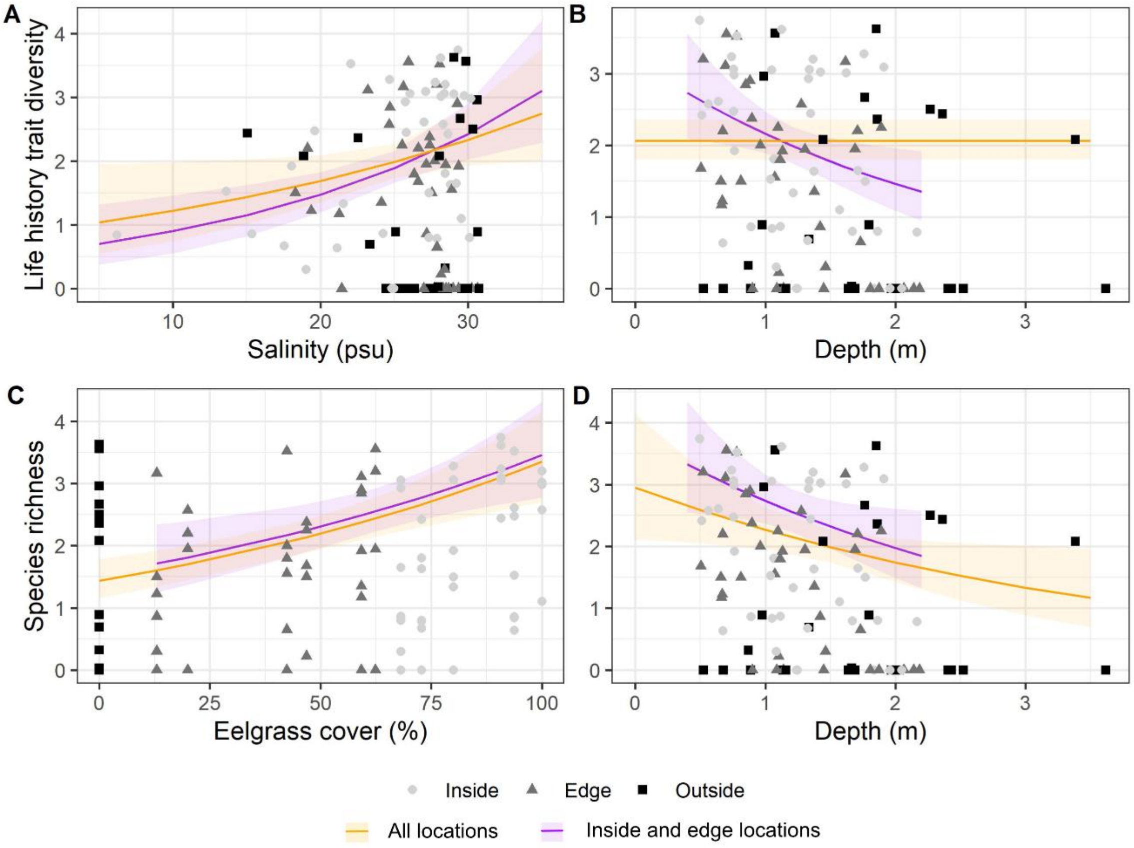

Figure 3.4: Relationship between life history trait (LHT) diversity and salinity (A) and water depth (B) and the relationship between species richness and eelgrass percent cover (C) and water depth (D). Orange regression line show trends using data from all locations (i.e., all transects) and purple regression line shows trends using data excluding outside locations (i.e., only edge and inside transects). Points represent the raw data and shaded area outlines the 95% confidence interval. Fish were sampled using a seine net survey sampling 500 m^2 per tow.

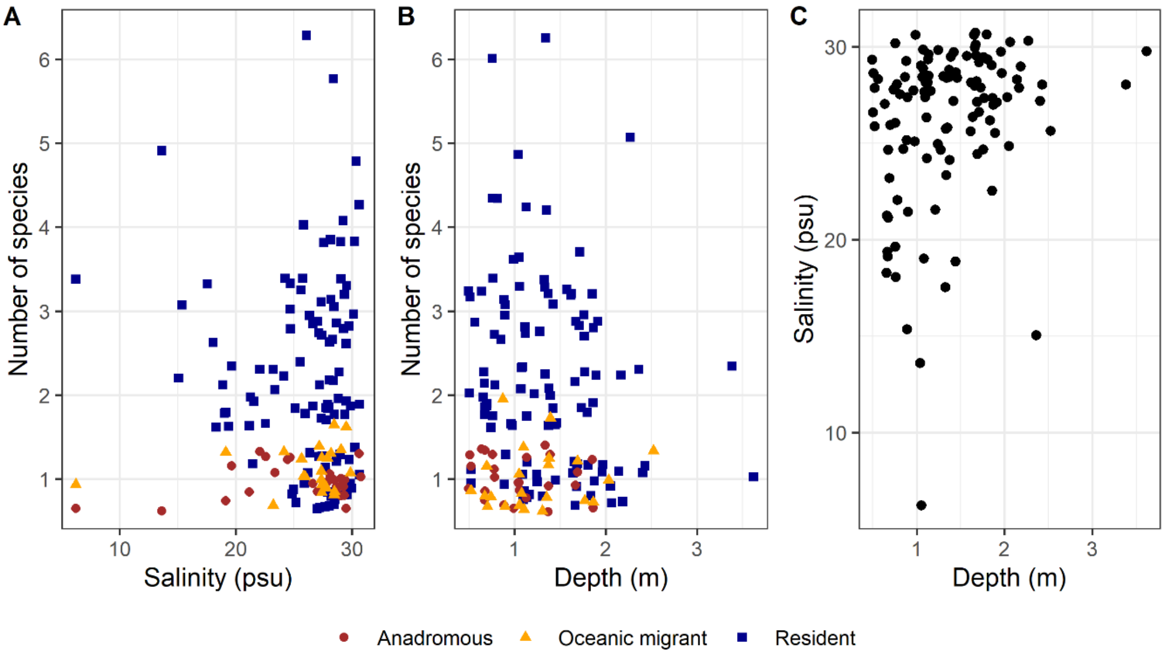

Figure 3.5: Relationship between species occurrence and water salinity (A) and depth (B), and the relationship between water salinity and depth (C) in three eelgrass meadows. Individuals are grouped according to movement life history traits, specifically whether the reside in eelgrass year round (resident) or migrate between freshwater and saltwater environments (anadromous) or from offshore into the coastal zone (oceanic migrant). Fish were sampled using a seine net survey sampling 500 m^2 per tow. Points were jittered to better visualize clusters.

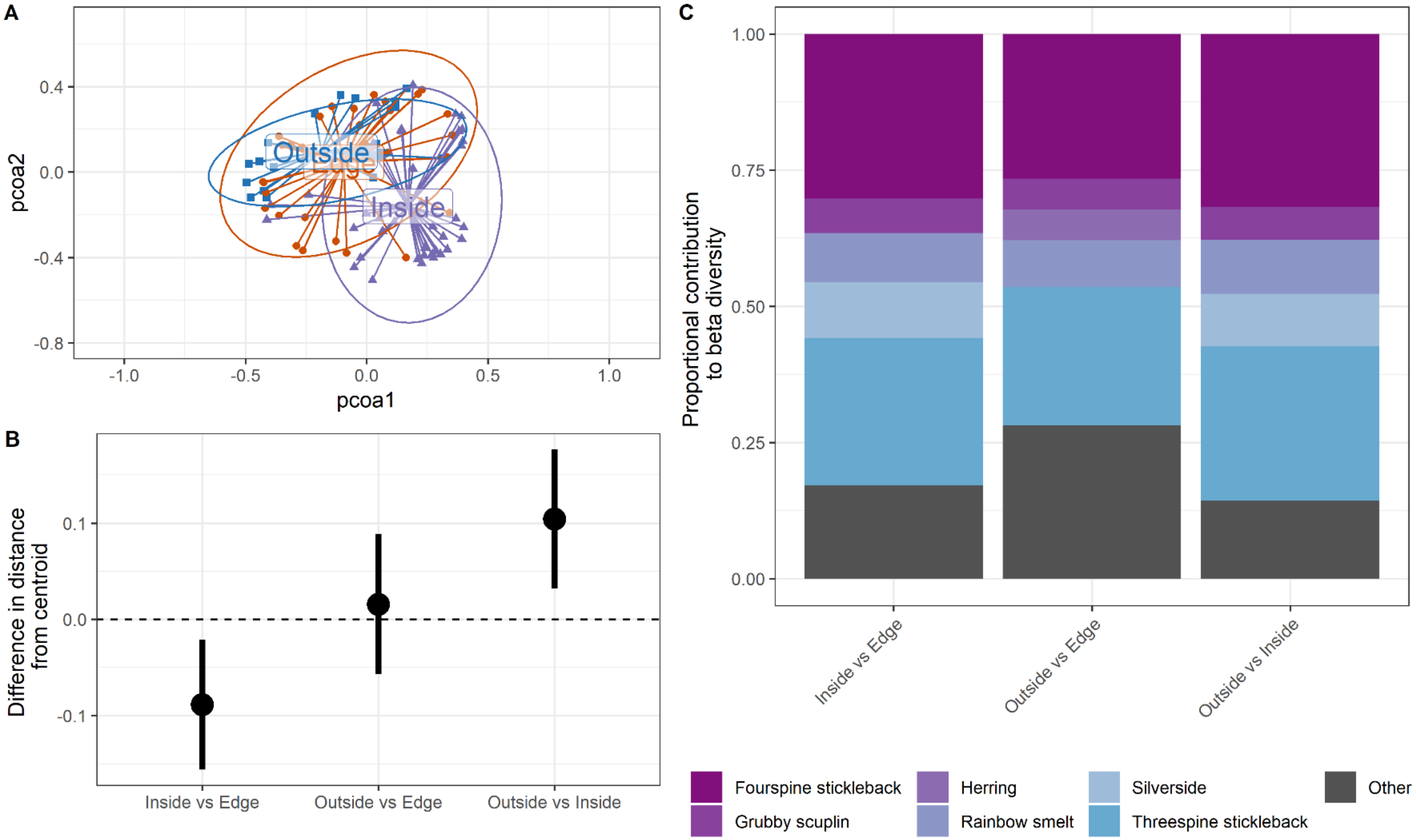

Figure 3.6: Ordination plot (A) and 95% confidence intervals (B) comparing the variability in fish composition, and the contribution of each species to the Bray-Curtis dissimilarity index (C) among locations inside, edge, and outside of all three eelgrass meadows. Differences shown in panel B represent the mean distance from centroid of the first location minus the second location in the x-axis label (e.g., inside vs edge represents inside – edge). Fish were sampled using a seine net survey sampling 500 m^2 per tow.

Chapter 4: The role of seagrass meadows in the coastal filter in a temperate boreal system

4.1 Abstract

By trapping nutrients, coastal ecosystems serve as a coastal filter between land and the open sea. Seagrasses act as important contributors to the coastal filter by removing nutrients from the water and trapping sediments. Understanding the processes and environmental conditions underpinning variability in nitrogen and carbon retention among and within seagrass meadows is important to evaluate the role of seagrass meadows in the coastal filter across geographic regions, especially in less studied regions. This study evaluates the role of eelgrass (*Zostera marina*) meadows in the coastal filter in boreal Newfoundland and Labrador, Canada, and identifies environmental traits that best predict variability in nutrient fluxes. I measured the proportions and stable isotopic composition of organic carbon (C_{org}) and nitrogen (N) in the surface sediment (top 5 cm) of three eelgrass meadows, where sediment cores were collected from different locations (i.e., inside, edge, outside) relative to each meadow. Sediment %N (0.22%), %C_{org} (2.82%), and C_{org} stock (11.1 Mg C_{org} ha^{-1}) were elevated in my study sites; however, nutrient content was not consistently higher inside the meadow than at the edge or outside. Variability in nutrient retention was best explained by a negative relationship with sediment bulk density. Additionally, differences in isotopic $\delta^{13}C_{org}$ enrichment between eelgrass tissue (-11.6‰) and sediment (-22.1‰) within sites indicated that nutrients were predominantly derived from allochthonous marine sources, where variability was best explained by salinity. By

measuring coastal filter processes in a new region and describing the mechanisms underlying functional variability, this study improves understanding of the contribution of eelgrass to nutrient cycles in the coastal zone and the potential of eelgrass as a blue carbon ecosystem.

4.2 Introduction

The coastal filter – coastal ecosystem processes that trap nutrients in the coastal zone (Asmala et al. 2017; 2019) – mitigates the detrimental impacts of eutrophication, elevated carbon dioxide (CO_2) concentration, and plastic pollution (Sanchez-Vidal et al. 2021), and contributes to primary productivity along the coastal shelf (McGlathery et al. 2007; Bouwman et al. 2013). Existing at the land-sea interface, seagrass contribute to the coastal filter by trapping particles and taking up nutrients, such as carbon and nitrogen, from allochthonous sources including terrestrial and freshwater discharge into the ocean (Bouwman et al. 2013; Asmala et al. 2017; Carstensen et al. 2020). Despite their importance, accelerating changes in climate and land-use increasingly degrade coastal ecosystems worldwide, threatening their filtering capacity (Lotze et al. 2006; Halpern et al. 2008). Conservation and restoration measures are on-going (Bayraktarov et al. 2015; United Nations 2015; Government of Canada 2022b), and are increasingly motivated by the need to offset CO_2 emissions. However, conserving seagrass' contribution to the coastal filter is challenging. These challenges include variability in the factors that drive the role of seagrass in the coastal filter, such as the efficiency of different species and the effects of biogeochemical conditions on nutrient uptake and particle deposition (Carstensen et al. 2020). Therefore, identifying traits within seagrass meadows that increase coastal filter efficiency will improve our understanding of the nutrient cycles in coastal systems and the potential of seagrass as a blue carbon ecosystem.

Seagrass meadows receive nutrients from marine sources via currents and tidal pulses and from terrestrial sources through freshwater runoff and erosion (Bauer et al.

2013). Acting as important contributors to the coastal filter (McGlathery et al. 2007; Duarte and Krause-jensen 2017), seagrass blades reduce wave and current action thereby increasing sedimentation and the blades, roots and rhizomes reduce particle resuspension (Gacia and Duarte 2001; Hendriks et al. 2008). Seagrasses also modify nutrient flux by metabolizing nutrients via photosynthesis and burying nutrients, as well as by exuding nutrients through their tissues and decomposition (Ziegler and Benner 1999; Aoki et al. 2020). When nutrients are exuded, they become bioavailable for heterotrophs which subsequently excrete the nutrients back into the system or transport them elsewhere via movement or trophic interactions (Hemminga et al. 1991; McGlathery et al. 1998; Ziegler and Benner 1999). When seagrass meadows bury nutrients, their anoxic sediment slows decomposition of organic matter resulting in nutrients becoming sequestered for decades to millennia (Mateo et al. 1997; McLeod et al. 2011). In fact, seagrass meadows are globally recognized among the most significant blue carbon habitats, storing an estimated 4.2-19.9 Pg of organic carbon globally (Fourqurean et al. 2012) at an approximate rate of 83.0 g C m^{-2} y^{-1} (Duarte et al. 2005). However, the contribution of seagrass as a coastal filter is known to show high spatiotemporal variability (Mazarrasa et al. 2018; Asmala et al. 2019; Carstensen et al. 2020). For instance, carbon stock estimates in temperate regions alone vary between 318 and 26,523 g C m^{-2} in the surface 25 cm and between 23.1 and 351.7 Mg C ha^{-1} in the top 1 m of sediment (Röhr et al. 2018). Similarly, variability is observed within individual estuarine systems, where carbon stocks in the top 10 cm of sediment in eelgrass meadows can be more than ten times greater in meadows closer to the mouth of the estuary than eelgrass meadows in the lower parts of the estuary (Ricart et al. 2020). Therefore, more research characterizing the role of seagrass in the coastal filter and the mechanisms underpinning this ecosystem function is necessary to better understand the apparent variability in ecosystem service output.

The capacity of seagrass to trap and bind nutrients has been strongly linked to the surrounding biogeochemical environment (Röhr et al. 2016, 2018a; Asmala et al. 2019; Carstensen et al. 2020). Monitoring sediment organic carbon (C_{org}), nitrogen (N), and their isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) is an approach that can reveal mechanisms underpinning variability in coastal filter functioning. Carbon and nitrogen cycles are intrinsically linked, where greater metabolism of C_{org} increases biological productivity and therefore, the amount of N that can be processed into organic matter via assimilation (McGlathery et al. 2007; Asmala et al. 2017). Higher sediment nutrient content (e.g., C_{org} and N) inside a seagrass meadow compared to sediment outside indicate that seagrass contributes to nutrient accumulation (Aoki et al. 2020; Moksnes et al. 2021). Coupling the nutrient content data with isotopic signatures reveals the source of nutrients (Kennedy et al. 2010), further elucidating whether autochthonous (i.e., seagrass contributing the nutrients via photosynthesis and decomposition) or allochthonous (i.e., nutrients are from other sources) nutrients are accumulated. Several studies have associated environmental factors as drivers of variability in seagrass sediment C_{org} stock, including meadow configuration (e.g., patchy vs continuous; Ricart et al. 2015; Oreska et al. 2017), distance from the mouth of the estuary (Ricart et al. 2020), wave exposure (Moksnes et al. 2021), and sediment grain size among others (Mazarrasa et al. 2018; Röhr et al. 2018). By monitoring nutrient fluxes in the water column, Asmala et al. (2019) attributed higher nutrient cycling rates in seagrass meadows to more saline and nutrient-rich environments in the Baltic Sea.

Furthermore, the proportion of autochthonous and allochthonous carbon in the sediment varies between meadows and nutrient sources can be marine or terrestrially derived (Johannessen and Macdonald 2016; Röhr et al. 2018; Prentice et al. 2020; Ricart et al. 2020), suggesting that the mechanisms by which seagrasses contribute to the coastal carbon filter vary. Indeed, most studies to date have determined seagrass meadow sedimentary C_{org} to be predominantly derived from allochthonous sources (e.g., Kennedy et al. 2010; Ricart et al. 2015, 2020b; Oreska et al. 2018; Prentice et al. 2020); however, this is not consistent. For instance, autochthonous sources accounted for 60-81% of the seagrass sedimentary C_{org} in western Australia (Salinas et al. 2020) and 60-94% of the seagrass sedimentary C_{org} in 15% of 54 temperate meadows (Röhr et al. 2018). Therefore, describing the processes and biogeochemical conditions driving variability across geographic regions is important for understanding the provision of ecosystem services, such as supporting aquatic biodiversity and storing carbon.

Here, I evaluated the role of eelgrass (*Zostera marina*) meadows in the coastal filter in a boreal coastal ecosystem. This study took place in Placentia Bay, Newfoundland, Canada, where recent efforts to restore eelgrass meadows have been conducted due to observed decline caused by the introduction of invasive European green crab (*Carcinus maenas*) since 2007 (Matheson et al. 2016). The water in the bay flows in a counter-clockwise direction. Oceanographic conditions are influenced by the Labrador Current, which supplies cold, productive water from the Arctic, and the Gulf Stream supplies warm water from the Caribbean Sea and eastern coast of the United States. Embayments are influenced by local processes such as wind, tide, and freshwater inflow (Ma et al. 2012).

Despite a long history of research on eelgrass ecology in the region (e.g., Geissinger et al., 2022; Gotceitas et al., 1997; Thistle et al., 2010), the role of eelgrass in the coastal filter has never been assessed. To quantify the role of eelgrass in the coastal filter in a boreal system, this study sought to:

1. measure the C_{org} and N content as well as the C_{org} and N stable isotopes in the surface sediment (i.e., top 5 cm) of three eelgrass meadows.
2. determine which environmental variables best predict the variability in C_{org} and N fluxes among the three meadows.

4.3 Methods

4.3.1 Study area

I studied three eelgrass meadows in Placentia Bay: North Harbour (47°52.703'N, 54°4.971'W), Swift Current (47°52.878'N, 54°13.467'W), and Baie de l'Eau (47°25.602'N, 54°47.406'W) (Figure 4.1). The three meadows occur at similar depths (<2 m below chart datum) and grow in remote, sheltered inlets with limited human activity. A road contours half of the meadow in Baie de l'Eau, and there is a gravel road approximately 100 m north of North Harbour. Swift Current is located in the most developed region of the three sites, where there is a community < 1km from the meadow (population of 207; Statistics Canada 2022), but on the opposite side of the inlet. Freshwater entering the system is carbon-rich, as it primarily originates from boreal forest draining catchments (Khoo et al. 2023). Eelgrass at the three sites is exposed predominantly to semidiurnal tides and estuarine circulation with lower salinity at low tide and higher salinities at high tide. Additionally, parts of the shallow coastal waters freeze in the winter exposing the eelgrass to ice scouring. Eelgrass in Placentia Bay reaches peak density in late-summer/early-fall (Murphy et al. 2021; Prystay et al. 2023; Chapter 2 of this thesis).

4.3.2 Field sampling

Hydrographic parameters, sediment grain size composition, and eelgrass shoot percent cover and morphology (i.e., length and width) data were collected to assess potential biological and environmental factors influencing sediment C_{org} and N storage. Oceanographic parameters, specifically temperature, salinity, dissolved oxygen (DO), and turbidity (measure in Nephelometric Turbidity units; NTU), were collected every 15 minutes from August 20, 2022 to November 22, 2022 using a moored SeapHOx equipped with an ECO-NTU sensor (Sea-Bird Scientific™, Washington, USA). Sensors were deployed in each site as close to the eelgrass meadows as possible, while ensuring they remained submerged by >1 m at low tide (required for the sensors to function; Figure S2.1). According to the pressure recorded by the SeapHOx units, the sensors were never deeper than 4 m at high tide. Samples to assess sediment grain size composition and eelgrass shoot morphology were collected along six 50 m transects for each site. Transects were marked every 10 m and placed perpendicular to shore such that two intersected the middle of the meadows, two intersected the edge of the meadows, and two were located outside the eelgrass meadows. In August 2020, I conducted snorkel quadrat surveys using a 1 × 1 m quadrat divided into 10 × 10 cm grid to assess eelgrass percent cover every 10 m along each transect, starting 20 m from shore (i.e., four quadrats per transect; $n_{\text{quadrat/site}} = 24$; Figure S2.1). Percent cover was estimated as the number of grid cells containing eelgrass shoots rooted in the grid cell. Three intact eelgrass shoots were then collected from within each quadrat to measure blade length and width of the longest blade per shoot.

Two sets of sediment cores were collected from each site. One set was collected in 2019 ($n_{cores} = 54$) and used for sediment grain size sorting, the second set was collected in 2020 ($n_{cores} = 54$) and used to estimate nutrient proportions, namely organic carbon (%C_{org}), nitrogen (%N), and particulate inorganic carbon (PIC) and their stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$). For both sets, three sediment cores were collected between 20 m and 40 m along each transect with >1 m between each core. These were collected by manually pushing a 3.5 cm diameter polycarbonate tube until depth of refusal (<10 cm deep due to rocky and compacted sediment; Postlethwaite et al. 2018) and extracted by gently digging to the base of the core using a short-handle spade and plugging both ends of the core using rubber stoppers. All cores were stored upright during transportation to the lab. To identify the carbon sources in the sediment samples, three eelgrass shoots were collected randomly from within each meadow for comparison between the eelgrass tissue and sediment isotopic ratios. These samples were collected in October 2021 and were stored in acid washed falcon tubes on ice during transportation to the lab, where they were rinsed in Milli-Q water and freeze dried to maintain the biological and chemical properties.

Lastly, eelgrass meadow aerial extents were estimated using a DJI Matrice remotely piloted aircraft system (RPAS) and supervised image classification using random forest analyses. RPAS survey methods, analyses, and results are described in Prystay et al. (2023; Chapter 2 of this thesis). Non-eelgrass habitats were removed from the classified maps, and the eelgrass rasters were converted into polygons. The areal extent of each eelgrass meadow was then determined by calculating the total area of the eelgrass polygons using the *sf* package (Pebesma 2018) in R (R Core Team 2022).

4.3.3 Laboratory processing

4.3.3.1 Processing of biological and environmental drivers

Eelgrass blade length and blade width were measured from the longest blade of each shoot to the nearest millimeter. For sediment grain size analysis, sediment from the first set of cores was pushed out of the corer using a plunger and the top 5 cm was sliced into a tray. Sediment was then dried at 105°C for 6 hours before sorting using a series of sieves (63, 106, 250, 500, 1000, 1400, 2000, and 4000 μm) and shaken for ten minutes using a tower sieve shaker (Röhr 2019). This was used to calculate the mean size fraction of sediment < 63 μm (i.e., mud content; %) and degree of sorting (phi) for each transect according to the methods outlined in Folk and Ward (1957).

4.3.3.2 Processing of sediment for C, N, and their isotopic signatures

To measure sediment N and C_{org} content and their isotopic signatures, the second set of cores were processed immediately upon arrival to the lab from the field. The top 5 cm of the sediment was sub-sampled using a 20 mL syringe cut at one end, then placed on pre-weighed aluminum weight boats, and dried at 60°C for 48 hours (Röhr et al. 2018; Ricart et al. 2020). Dried samples were weighed to calculate sediment bulk density (g cm^{-3}; see *Supplementary Information S1 Equations for sediment variables*), then homogenized using an acid washed mortar and pestle before dividing the sample in half and storing each half in two separate acid washed falcon tubes. One half of the sample was acidified for C_{org} analysis and the other half was left untreated to avoid altering $\delta^{15}N$ values and to measure total carbon to calculate %PIC (Bunn et al. 1995; Howard et al. 2014; Schlacher and Connolly 2014). For the acidified samples, I added HCl 0.5M into the falcon tube and mixed it for 15 minutes using a vortex mixer. Samples were then left for 18-24 hours before decanting the acid using a disposable pipette and adding new acid until no effervescence (i.e., presence of carbonates) was detected. For all cases, one acid wash cycle was sufficient. Samples were then rinsed three times using Milli-Q water and centrifuged before decanting. Acidified samples were re-dried on new pre-weighed weight boats and re-homogenized using the same protocol as before. The proportional mass and stable isotope ratios for carbon and nitrogen were measured by pelletizing 10-57 mg of each sediment sample and processed using a Costech ECS 4010/Thermo DELTA V Advantage IRMS by the Bigelow Laboratory for Ocean Sciences Analytical Services. All samples fell within the analytical range for this method (Table S4.1).

4.3.3.3 Processing of eelgrass tissues

Eelgrass samples were freeze-dried and ground using a mortar and pestle and liquid nitrogen. Duplicates of each sample were analyzed, where 3 mg of each sample was pelletized and processed to measure $\%C_{org}$, %N, $\delta^{13}C_{org}$, and $\delta^{15}N$ using a Carlo-Erba NA1500 Elemental Analyzer by the Stable Isotope Lab of Memorial University. All tools used were cleaned using 70% ethanol before processing each sample.

4.3.4 Statistical analyses

C_{org} density (mg C_{org} cm^{-3}), C_{org} stock (Mg C_{org} ha^{-1}), and %PIC were calculated according to the equations outlined in *Supplementary Information S1 Equations for sediment variables*. The relationship between %C_{org}, %N, and molar C:N ratios, as well as the relationship between $\delta^{13}C_{org}$ and $\delta^{15}N$ were analyzed using Pearson's correlation. Given that %C_{org}, %N, and C:N ratios were strongly correlated, I only modeled environmental covariate relationships with %C_{org}, C_{org} density, and $\delta^{13}C_{org}$. Environmental parameters were estimated using the median water temperature, salinity, DO, and NTU for each site, and the mean eelgrass blade length, width, and percent cover for each transect. Sediment parameters, including sediment bulk density, degree of sorting, and silt content were measured for each core and were therefore not averaged. NTU was correlated with temperature and salinity and DO was correlated with temperature, and eelgrass blade length was correlated with eelgrass blade width ($r < -0.6$ or $r > 0.6$ were deemed colinear; Figure S4.1); therefore, NTU, DO, and eelgrass blade width were excluded as covariates in subsequent models.

I used separate models to determine whether % $C_{org,}$ C_{org} density, or $\delta^{13}C_{org}$ varied spatially, one with site as a fixed effect and one with transect location (i.e., inside, edge, outside of the eelgrass meadow) as a fixed effect, where transect ID was a random effect in both models. Each model was followed by multiple comparison analyses on the fixed effects using Bonferroni corrected 95% confidence intervals (Midway et al. 2020). Next, to assess whether environmental drivers, namely sediment bulk density, degree of sorting, silt content, median salinity, median temperature, and transect mean eelgrass blade length and percent cover, influenced the variability in C_{org} and N fluxes, I evaluated the relationship between $\%C_{org}$ and the environmental covariates using a beta regression generalized linear mixed model (GLMM) with a logit link given that $\%C_{org}$ is bound between 0 and 1. C_{org} density is continuous and positive, therefore I used a GLMM with a gamma distribution and log link function. In this case, sediment bulk density was excluded as a covariate given it is used to calculate C_{org} density. Lastly, I used a linear mixed effect model with a Gaussian distribution to evaluate the relationship between $\delta^{13}C_{org}$ and environmental drivers. All models included transect ID as a random effect to account for dependencies among cores collected in similar regions of the meadows. Finally, I used stepwise model selection using Akaike information criterion (AIC) to identify the most parsimonious model. Because outside transect data could not include measures of eelgrass blade length, each model was repeated twice. The first iteration included outside transect data but excluded eelgrass blade length as a covariate, whereas the second iteration excluded outside transect data and included eelgrass blade length as a covariate.

I could not run a mixture model analysis for the stable isotope data because I only had source values for eelgrass tissue $\delta^{13}C_{org}$ and $\delta^{15}N$. Instead, isotope ratios were compared to the eelgrass tissue levels isotopic signatures and $\delta^{13}C$ values from Khoo *et al.* (2023), where isotope values of suspended particles were collected from two sets of freshwater samples and two sets of saltwater samples collected from both Piper’s Hole and Come by Chance in Placentia Bay (Figure 4.1). Given that the three meadows are surrounded by forest and anthropogenic infrastructure (e.g., cottage or road), I expected terrestrial sources may include tree detritus, anthropogenic pollution, or bacteria. Potential marine allochthonous sources may include phytoplankton or bacteria, as observed in Khoo *et al.* (2023).

4.4 Results

All three sites exhibited similar oceanographic conditions (Figure 4.2). The average median daily salinity was 2.1 and 2.6 practical salinity unit (psu) lower in Swift Current (27.3 ± 1.6 psu; mean ± sd) than Baie de l'Eau (29.5 ± 1.6 psu) and North Harbour (29.9 ± 1.1 psu), respectively (mean ocean salinity is 34.7 psu). In contrast, NTU was highest in Swift Current, followed by North Harbour, and lowest in Baie de l'Eau; however, on average all three sites had low turbidity (<1 NTU). Eelgrass morphology and sediment characteristics also differed among sites (Table 4.1), where eelgrass blade length and width were highest in Swift Current and lowest in North Harbour, but blade percent cover was on average 15-17% lower in Swift Current compared the other two sites. Sediment mud content and sediment bulk density differed the most among sites and varied within all three sites. In general, mud content was lowest in North Harbour but comparable in Swift Current and Baie de l'Eau, whereas sediment bulk density was lowest in Swift Current but comparable between North Harbour and Baie de l'Eau.

Overall, surface sediment in each site contained on average 0.22 ± 0.19 %N (mean ± sd) and 2.82 ± 2.89 %C_{org}, and >99 % of the carbon in the surface sediment was organic. The %C_{org} in the top 5 cm of sediment was on average 1.7% higher in the eelgrass meadow (i.e., edge and inside) compared to outside the meadow (Figure 4.3). Only two samples contained measurable proportions of PIC, which were collected from an outside transect in

Baie de l'Eau (2.0%) and an inside transect in Swift Current (1.3%). Although %N and %C_{org} were strongly correlated (Figure 4.4A), %N did not vary nearly as much as C_{org} and did not differ inside the meadow compared to outside (0.1% difference). %C_{org} and C_{org} density did not statistically differ between sites and significant differences in %C_{org} and C_{org} density were only observed between North Harbour inside and outside locations (Figure 4.5). North Harbour had the highest %C_{org} and C_{org} density inside the meadow, Swift Current at the edge, and Baie de l'Eau outside the meadow (Figure 4.5).

4.4.1 Relating carbon to environmental variables

Based on the most parsimonious models according to AIC scores, sediment bulk density and eelgrass percent cover best explained the variability %C_{org}, and therefore, also %N, and C:N ratios given their strong correlation (Figure 4.4A,B; Figure 4.6). Specifically, %C_{org} was negatively related to sediment bulk density (GLMM: df = 49, Z= -9.7, p-value < 0.001; Figure 4.6A; Tables S4.2, S4.3). In contrast, %C_{org} was positively related to eelgrass percent cover (Figure 4.6B). However, despite its inclusion in the most parsimonious model indicating that eelgrass percent cover explained variability in %C_{org}, this relationship was not statistically significant (GLMM: df = 49, Z = 1.9, p-value = 0.06; Figure 4.6B). Sediment bulk density was generally lower where eelgrass percent cover was greater, however the two habitat traits were not correlated (r = 0.14; p-value = 0.31). Interestingly, C_{org} density (19.9 ± 13.9 mg cm^{-3}) was not statistically related to any of the environmental variables measured. When restricting the data to only examine inside and edge transects (i.e., when eelgrass was present to avoid false zeros within outside transects), neither C_{org} density nor %C_{org} were related to eelgrass blade length (Table S4.3). In this case, sediment mud content was included in the most parsimonious model for % C_{org}, however it did not have a statistically significant effect.

Variability in the isotopic composition of carbon (i.e., $\delta^{13}C_{org}$; -22.2 ± 1.6 ‰), which was positively correlated with sources of nitrogen (i.e., $\delta^{15}N$; 3.9 ± 1.1 ‰; Figure 4.4C), was best explained by salinity (Figure 4.6C; Table S4.2). Temperature, sediment bulk density, mud content, and eelgrass percent cover were also included as covariates in the most parsimonious model; however, only salinity had a statistically significant effect (GLMM: df = 46, Z= -4.7, p-value < 0.001). Specifically, $\delta^{13}C_{org}$ was more depleted in more saline systems. Comparing $\delta^{13}C_{org}$ against source data from Khoo *et al.* (2023) suggests surface sediment in and around each eelgrass meadow was a combination of terrestrial and marine derived sources, but predominantly marine derived (Figure 4.7A). This was supported by the C:N ratio, which also overlapped with the marine and terrestrial source C:N ratios reported in Khoo *et al.* (2023), and in some cases even overlapped with the eelgrass C:N ratio (i.e., Swift Current) and the Redfield ratio for plankton (C:N of 6.6; Redfield 1958) (Figure 4.7B). However, C_{org} was predominantly supplied from marine sources other than the eelgrass themselves, given that $\delta^{13}C$ in the seagrass tissue (-11.64 ± 1.8 ‰) was overall ~10‰ more enriched than the surface sediment (Figure 4.7A). The C:N ratios were similar among sites, with the largest variability observed in Swift Current (Figure 4.7B). For North Harbour and Swift Current, the C:N ratio was also generally lower outside the meadow compared to the edge and inside (Figure 4.7B).

4.4.2 Sediment carbon content at the meadow scale

Baie de l'Eau had the largest eelgrass area, which was over four-fold larger than North Harbour (Table 4.2). Although Swift Current was calculated to have covered less area than Baie de l'Eau, the meadow extended beyond my RPAS survey and therefore the eelgrass area and estimated C_{org} stock are only representative of a portion of the eelgrass meadow. C_{org} density and C_{org} stock were highest in Baie de l'Eau. North Harbour had the smallest eelgrass blades (Table 4.1) and lowest %C_{org}. However, sediment bulk density was higher than in Swift Current and comparable to Baie de l'Eau, resulting in North Harbour containing the highest C_{org} density and comparatively high C_{org} stock given the smaller meadow size. Overall, when extrapolated to the meadow scale, the average total C_{org} stock in the surface sediment (i.e., top 5 cm) of the three eelgrass meadows was 11.6 Mg C_{org} ha^{-1} (Table 4.2).

4.5 Discussion

This study provides an evaluation of the role of eelgrass in the coastal filter in a boreal ecosystem located in Newfoundland, Canada. Similar to previous research on nutrient storage in seagrass meadows (Röhr et al. 2016, 2018a; Mazarrasa et al. 2018; Asmala et al. 2019), C_{org} and N retention in the coastal zone was related to environmental parameters, particularly sediment bulk density. However, I also show that differences in nutrient retention could not be solely explained by variability in eelgrass traits or environmental parameters. Neither could these differences be attributed to carbon reintroduction into the food web, as C:N ratios, which indicate the refractory nature of organic material

(Grebmeier et al. 1987; Ramey and Snelgrove 2003), were similar among meadows. Furthermore, also consistent with most seagrass meadow studies (e.g., Kennedy et al. 2010; Ricart et al. 2015; Oreska et al. 2018; Prentice et al. 2020), the majority of the C_{org} input did not originate from the eelgrass tissues themselves. Instead, I found that allochthonous carbon inputs were dominantly marine derived and best predicted by salinity, implying relatively low riverine sediment discharge into the study sites. Despite previous observations of variability in coastal filter function (Asmala et al. 2019) and C_{org} stocks observed in other regions (e.g., Ricart et al., 2020; Röhr et al., 2018), my results did not indicate significant variability in surface sediment $\%C_{org}$ and %N content, and sources across seagrass meadows, suggesting low variability in coastal filter functioning between eelgrass habitats in Placentia Bay. Nevertheless, small differences in nutrient retention measured at small scales manifested into larger differences in nutrient stock in the surface sediment when extrapolated to the meadow scale.

Each of the three meadows in this study contained high proportions of $\%C_{org}$ (2.82 ± 2.89, mean ± SD) compared to literature values for *Zostera marina* (e.g., < 1.3% [western Canada; (Postlethwaite et al. 2018; Prentice et al. 2020)], 0.13-5.78% [Baltic Sea; Röhr et al. 2016]), and coincidingly, high C_{org} stocks (11.1 ± 6.2 Mg C_{org} ha^{-1}). Whereas the average C_{org} stock in temperate systems is estimated to be 27.2 Mg C_{org} ha^{-1} in the upper 25 cm of sediment (Röhr et al. 2018), when divided by 5 (to match the 5cm depth measured in the present study) this estimate yields 5.4 Mg C_{org} ha^{-1}, which is approximately half the mean C_{org} stock estimates in the current study. This is also the case when I compare C_{org} stocks in my study to estimates of eelgrass C_{org} stock along the Pacific coast of North

America, with a remarkably low average of 18.46 Mg C_{org} ha^{-1} in the surface 25cm of sediment (divided by 5 amounts to 3.7. Mg C_{org} ha^{-1}; Prentice et al., 2020). Also, an important difference between my study and others was that the sampling depth was shallower than most previous studies due to a shallow depth of refusal in my sites. Therefore, the outlined differences between this study and others represent rough comparisons given the relationship between depth and sediment carbon levels is inconsistent as most seagrass cores show a mixed depth profile in C_{org} density (Röhr et al. 2016; Kindeberg et al. 2019; Potouroglou et al. 2021). Other studies have also reported C_{org} proportions reaching close to 6% in the top 3cm of seagrass sediment in Australia (Ricart et al. 2020), and C_{org} density close to 50 mg C_{org} cm^{-3} within the top 5 cm (Röhr et al. 2016), exceeding levels measured in my study. Furthermore, sediment C_{org} stock within the surface 5 cm can be highly variable, such as ranging between 0.83 to 10.89 Mg C_{org} ha^{-1} along the central Canadian Pacific coast (Prentice et al. 2019), an upper limit that is similar to the C_{org} stock observed in my study. The high C_{org} content measured in this study may be because my study sites were located in sheltered embayments (Figure 4.1) and close to the mouth of estuaries, both factors that have been suggested to promote higher sediment C_{org} concentrations in other studies (Röhr et al. 2016; Prentice et al. 2019, 2020; Ricart et al. 2020). Measures of C_{org} accumulation and more detailed source data would better elucidate the mechanisms driving the higher carbon content in the three meadows.

My results identified that C_{org} concentration was best explained by sediment bulk density. Sediment parameters, including bulk density, have been associated with C_{org} storage in eelgrass meadows previously, including in temperate regions (Gullström et al.

2018; Röhr et al. 2018; Dahl et al. 2020). The negative relationship between %C_{org} content and sediment bulk density has been attributed to low density of hydrated organic material (Avnimelech et al. 2001). Sediment bulk density is also affected by hydrodynamic exposure, which induces sediment compaction (Dahl et al. 2020), while also introducing and exporting organic material from the system thereby affecting nutrient accumulation (Bauer et al. 2013; Röhr et al. 2018).

A mechanism explaining the high capacity of eelgrass meadows to retain nutrients is that eelgrass blades extend into the water column, reducing wave and current exposure, which promotes vertical accretion and particle retention (Hendriks et al. 2008; Duarte et al. 2010; Asmala et al. 2019). Despite evidence linking eelgrass to %C_{org} and %N accumulation, the high levels of nutrients in this study could not be consistently attributed to the presence of eelgrass in the sites. Based on previous studies (Ricart et al. 2015; Mazarrasa et al. 2018), I expected %C_{org} and C_{org} density to be highest inside the meadow, followed by the edge then lowest outside the meadow. However, while this pattern was apparent for North Harbour it was not apparent in the other two sites or when data from all three sites were pooled together. This may be due to differences in meadow configuration, where more continuous meadows tend to store more C_{org} in the middle of the meadow and patchier meadows tend to be variable (Ricart et al. 2015, 2020) or simply less efficient at C_{org} storage (Röhr et al. 2018). Alternatively, the ability to identify a negative relationship between C_{org} storage and distance from the interior of the meadow may be scale dependent. Therefore, another likely explanation for lack of spatial differences in nutrient storage is that the non-vegetated samples for both Swift Current and Baie de l’Eau were collected too close to the meadows. In doing so, I may have either sampled sediment where seagrass used to be, resulting in higher C_{org} levels, or the non-vegetated samples were affected by C_{org} “overflow” from the meadow (i.e., underground carbon transport; Kennedy et al. 2010; Postlethwaite et al. 2018). Determining the spatial scale at which eelgrass meadows affect nutrient storage in the sediment is important for understanding how far reference samples should be collected to ensure effective evaluation of the role of eelgrass in the coastal filter.

Seagrass meadows contribute autochthonous C_{org}, supplied through seagrass senescence and exudation (Ziegler and Benner 1999; Kennedy et al. 2010). However, eelgrass tissue in this study was ~10‰ more carbon enriched than nearby sediment $\delta^{13}C_{org}$, matching similar $\delta^{13}C_{org}$ and $\delta^{15}N$ values observed in eelgrass tissue collected at similar latitudes elsewhere (Hemminga and Mateo 1996; Hitchcock et al. 2017). The elevated tissue carbon enrichment suggests that the sediment C_{org} was predominantly derived from marine sources other than eelgrass, such as marine bacteria and phytoplankton (Boschker and Middelburg 2002; Savoye et al. 2003; Bianchi and Canuel 2014). However, the presence of high allochthonous sources is generally coupled with high water turbidity, which was not the case in my study sites (Ricart et al. 2020). Instead, $\delta^{13}C_{org}$ (i.e., C_{org} sources) were best explained by salinity. Elevated salinity affects C_{org} stocks by increasing productivity or inducing salinity stress, promoting tissue breakdown (Boström et al. 2014; Salo et al. 2014). However, this does not explain its effect in sites where $\delta^{13}C_{org}$ is more enriched compared to terrestrial sources or eelgrass tissue. Therefore, given that salinity also affects water density and alters ionic strength between organic matter compounds, I suggest that salinity is more likely affecting flocculation (i.e., particles sink vs remain suspended in the water column) in the estuaries (Khoo et al. 2022). Specifically, flocculation rates are likely higher in the more saline sites (North Harbour and Baie de l'Eau), increasing the contribution of enriched $\delta^{13}C_{org}$ marine sources to the sediment C_{org} stock at these locations.

Variability in nutrient retention in an ecosystem will lead to nutrient stocks that are independent of meadow size. In this study, the eelgrass in North Harbour contained a higher C_{org} density than the Baie de l'Eau meadow. Consequently, when extrapolating C_{org} stock in the surface sediment to the meadow scale, North Harbour is 22% more efficient at retaining nutrients than Baie de l'Eau, despite covering a smaller area. Although I identified that nutrient stock differences in Placentia Bay eelgrass meadows were affected by sediment bulk density, I also show that the source of C_{org} was predominantly marine derived. Therefore, other environmental mechanisms not included in this study may also be affecting the observed variability in C_{org} stock. For example, other studies have attributed variability in C_{org} storage in eelgrass meadows to hydrodynamic exposure (Röhr et al. 2016; Prentice et al. 2019; Dahl et al. 2020). Whereas greater wave and current exposure can increase sediment compaction and accumulation of C_{org}, such exposure can also export eelgrass and other nutrient sources from the coastal zone. Additionally, the interactions between eelgrass and grazers can also affect nutrient accumulation in a meadow (Mazarrasa et al. 2018; Villnäs et al. 2019). The C:N ratio indicates the food quality in the sediment, with higher ratios indicating less degradable (i.e., lower quality) organic material that is more resistant to microbial degradation (Grebmeier et al. 1987; Ramey and Snelgrove 2003). In my sites, the ratio of bioavailable nutrients (C:N) was consistent across meadows, suggesting comparable metabolic processing by coastal microbial communities. Further, most of the enriched C:N ratios in North Harbour and Swift Current were outside the meadow and the degraded ratios were inside and at the edge. This implies that eelgrass is also contributing to the metabolic activity in the system, thereby facilitating nutrient re-introduction into the food web.

4.5.1 Conclusion

Seagrasses hold socio-economic value by sequestering carbon and nitrogen, and biological value by supplying nutrient-rich habitat that supports the coastal food web. This study contributes to the understanding of the role of eelgrass in the coastal filter by providing the first estimates C_{org} and nitrogen content in the surface sediment of eelgrass meadows in boreal Newfoundland and Labrador. I revealed that these meadows are carbon rich where carbon is predominantly derived from marine allochthonous sources, likely marine bacteria and phytoplankton. Additionally, I show that, in systems where terrestrial sources are low, coastal filter functioning may be enhanced in meadows with low sediment bulk density. By quantifying eelgrass carbon and nitrogen storage in a new region and describing the mechanisms underlying their variability, findings from this study will benefit future eutrophication mitigation and blue carbon estimation in the coastal zone, both nationally and globally.

Table 4.1: Eelgrass morphology and sediment characteristics. Measurements are presented as means ± standard deviation. Eelgrass morphology was calculated according to measurements from three eelgrass shoots per quadrat, where there were four quadrats per transect and six transects per site. Eelgrass percent cover was calculated according to the average density in each transect. Sediment parameters were calculated according to the average of each sediment core, where there were three sediment cores collected per transect and six transects per site.

Site	Eelgrass			Sediment		
	Blade length (mm)	Blade width (mm)	Blade percent cover (%)	Degree of sorting (phi)	Mud content (<63 μm)	Bulk density (mg mL^{-1})
Baie de l’Eau	375.0 ± 114	3.3 ± 0.6	49.3 ± 38	1.83 ± 0.3	3.31 ± 2.6	1.30 ± 0.4
North Harbour	294.5 ± 111	2.2 ± 0.4	47.4 ± 42	1.86 ± 0.07	1.91 ± 1.4	1.25 ± 0.5
Swift Current	377.1 ± 244	3.7 ± 1.7	32.4 ± 31	1.80 ± 0.2	3.66 ± 2.4	0.78 ± 0.5

Table 4.2: Carbon density and carbon stock (mean ± SE) integrated for a depth profile of 5 cm. Location "Total eelgrass only" was estimated using cores collected from inside and edge transects only (omitting outside transect cores). See Supplementary Information (section Appendix C section C1. Equations for sediment variables) for equations used to calculate C_{org} density and C_{org} stock. Asterix (*) signifies that only a portion of the meadow was mapped and therefore estimates of C_{org} are only representative of the portion mapped rather than the full meadow area.

Site	Location	Number of sediment cores	C_{org} density ($mg\ C_{org}\ cm^{-3}$)	C_{org} stock ($Mg\ C_{org}\ ha^{-1}$)	Eelgrass area (ha)	Total C_{org} stock (Mg)
North Harbour	Inside	6	29.7 ± 6.2	14.9 ± 3.1		
	Edge	6	19.3 ± 5.8	9.6 ± 2.9		
	Outside	6	3.8 ± 0.9	1.9 ± 0.5		
	Total	18	17.6 ± 3.7	8.8 ± 1.9		
	Total eelgrass only	12	**24.9 ± 4.4**	**12.2 ± 2.2**	6.54	**80.1 ± 14.2**
Swift Current	Inside	6	20.6 ± 2.2	10.3 ± 1.1		
	Edge	6	25.4 ± 4.4	12.7 ± 2.2		
	Outside	6	13.2 ± 5.0	6.6 ± 2.5		
	Total	18	19.7.8 ± 2.5	9.9 ± 1.3		
	Total eelgrass only	12	**23.0 ± 2.4**	**11.5 ± 1.2**	11.20*	**128.9 ± 13.7***
Baie de l'Eau	Inside	6	19.7± 4.3	9.8 ± 2.2		
	Edge	6	18.4 ± 6.5	9.2 ± 3.2		
	Outside	6	28.6 ± 7.4	14.3 ± 3.7		
	Total	18	22.2 ± 3.5	11.1 ± 1.8		
	Total eelgrass only	12	**19.0 ± 3.7**	**9.5 ± 1.9**	25.41	**241.9 ± 54.8**

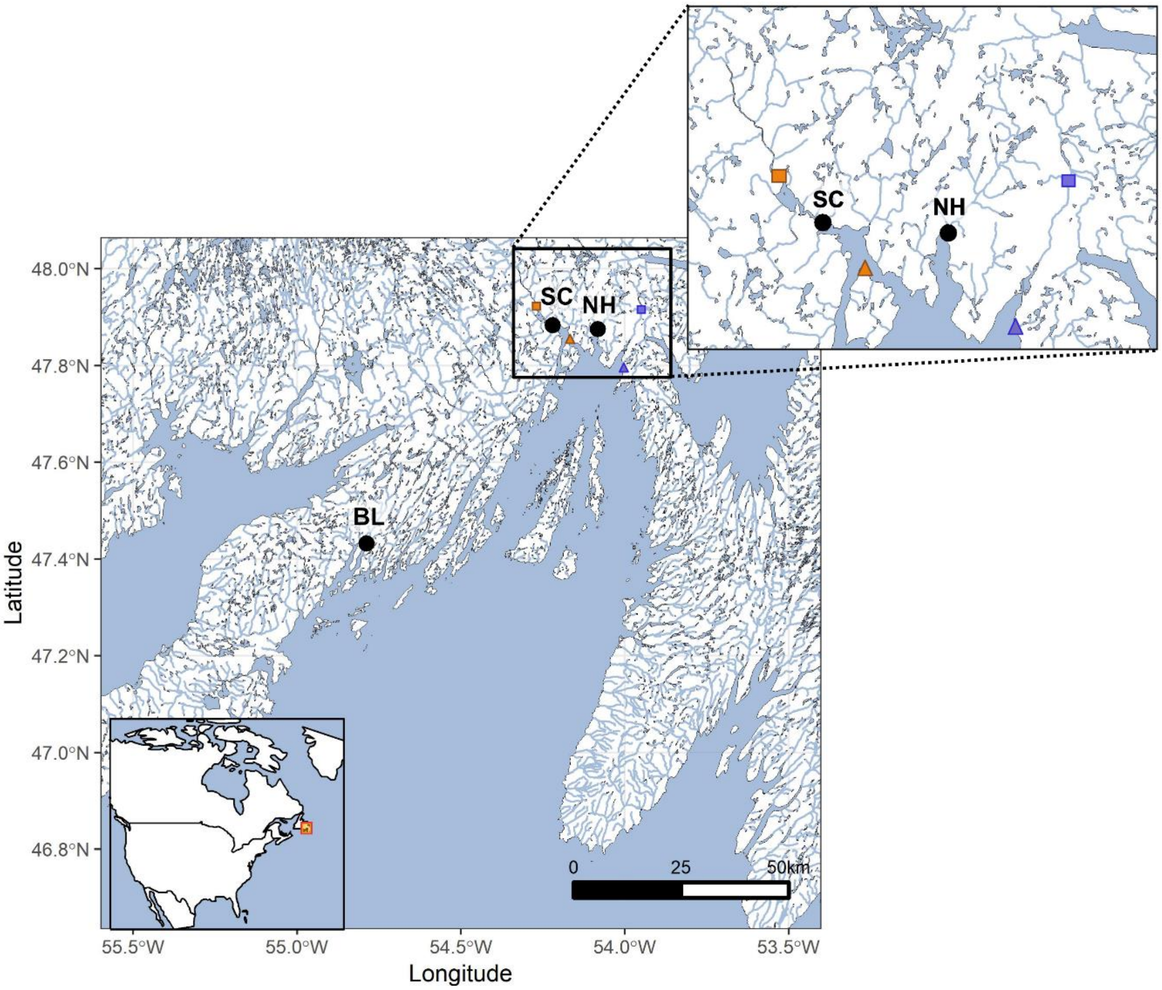

Figure 4.1: Map of study sites. Black circles represent the three eelgrass meadows studied: Baie de l'Eau (BL), Swift Current (SC), and North Harbour (NH). Source data used to compare stable isotope levels were collected from Piper's Hole (orange) and Come by Chance (purple), where squares symbolize freshwater sources and triangles symbolize saltwater sources.

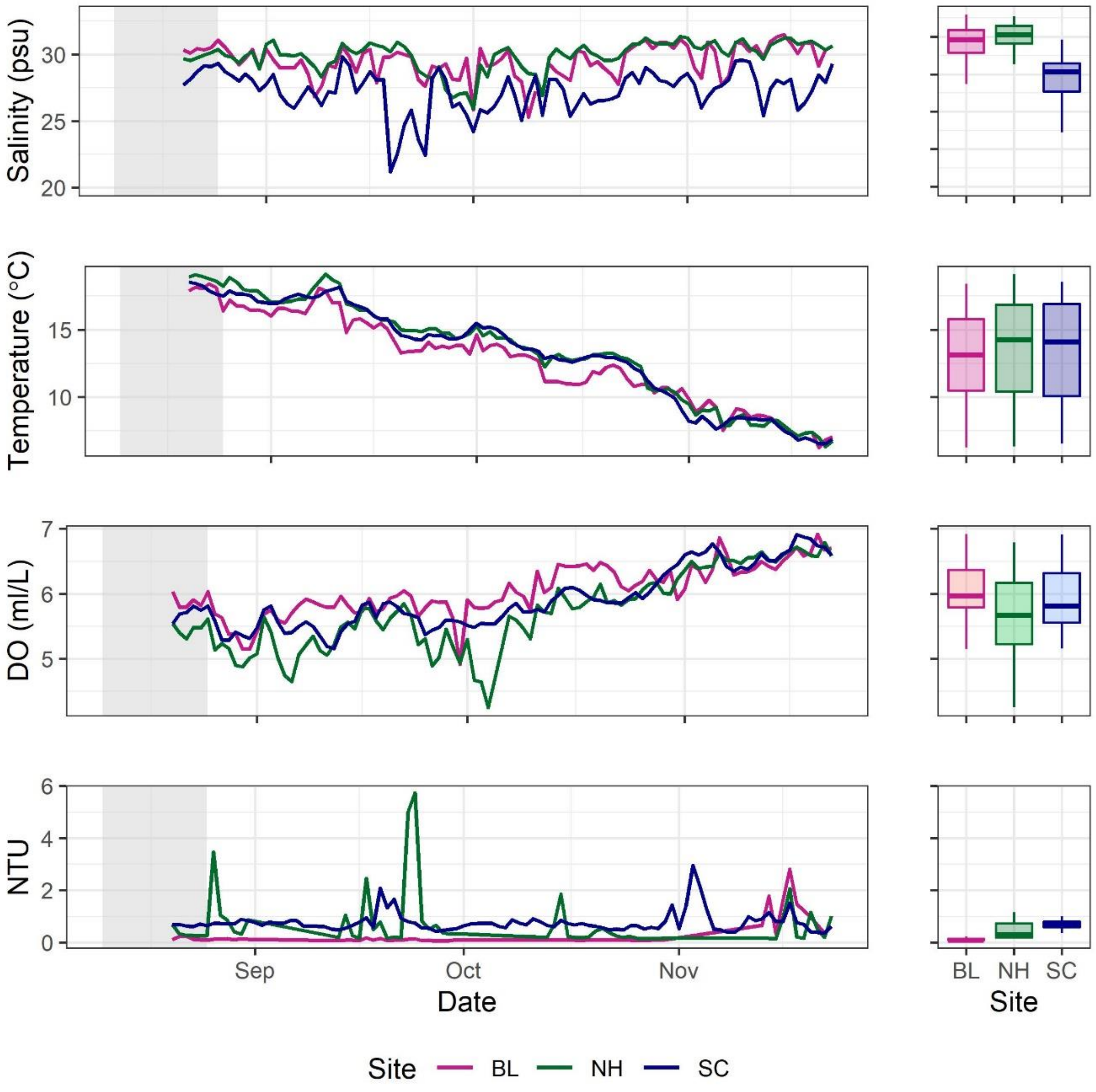

Figure 4.2: Mean daily water salinity, temperature, dissolved oxygen (DO), and turbidity (nephelometric turbidity unit (NTU)) in three eelgrass meadow sites, Baie de l'Eau (BL), North Harbour (NH), and Swift Current (SC), from August 20, 2022 to November 22, 2022. Boxplots show the median daily averages used in the statistical models. Grey shaded areas represent the time period when sediment sampling occurred.

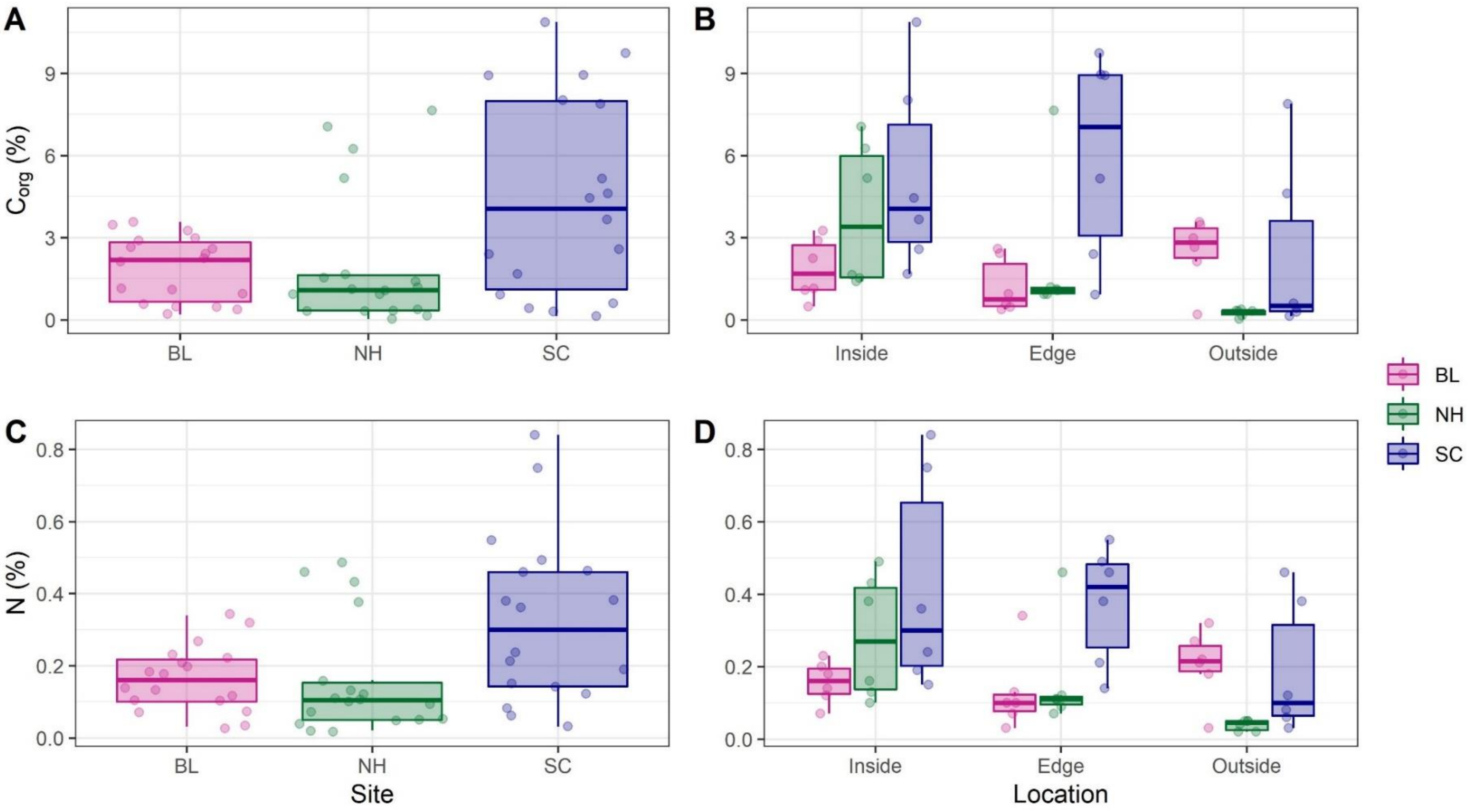

Figure 4.3: Boxplot showing the C_{org} (A, B) and N (C, D) content in the top 5 cm of sediment in three eelgrass meadows, Baie de l'Eau (BL), North Harbour (NH), and Swift Current (SC), in Placentia Bay, Newfoundland. Panels A and C include pooled data from all transect locations. Location refers to the location where the sediment samples were collected relative to the eelgrass meadow. Points represent the raw data and were jittered along the x-axis for visualization.

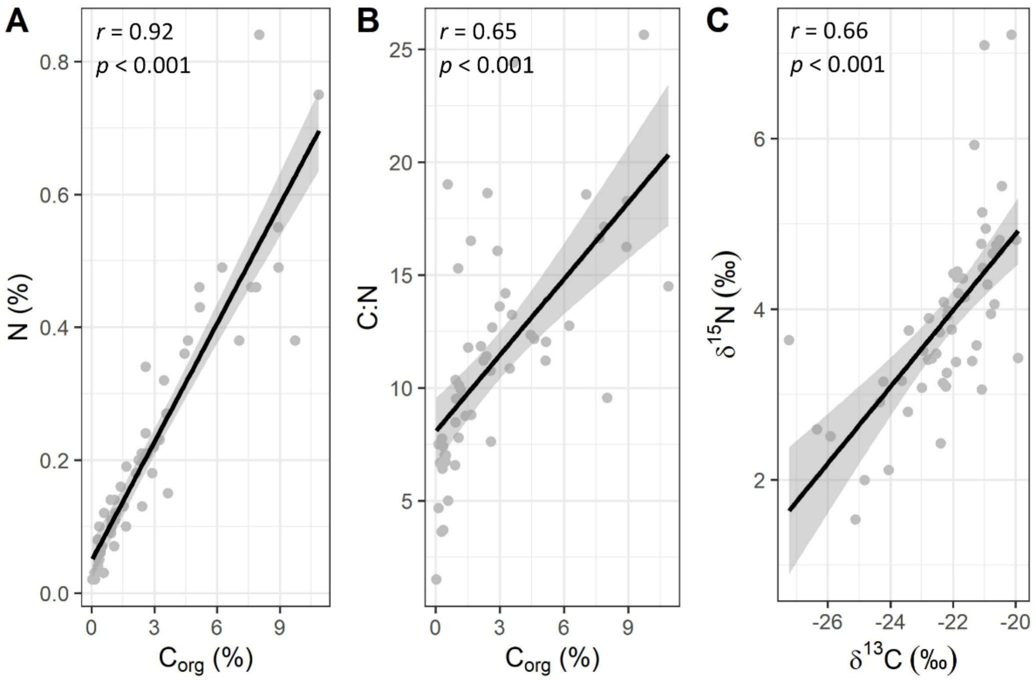

Figure 4.4: Correlation between C_{org}, N, and C:N in the top 5 cm of sediment in three eelgrass meadows in Placentia Bay, Newfoundland.

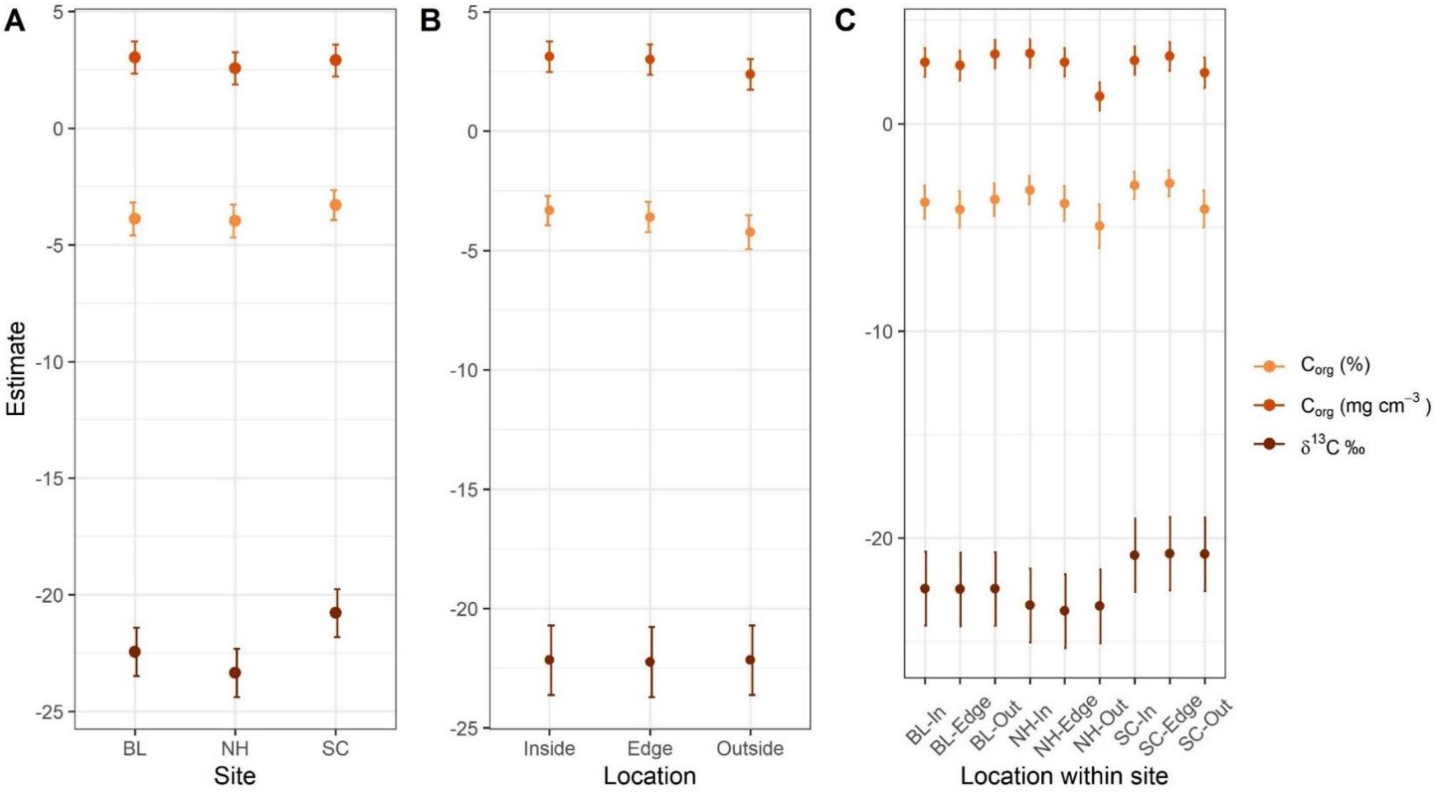

Figure 4.5: Bonferroni corrected 95% confidence intervals for linear regression models comparing C_{org} (orange), C_{org} density (red), and δ^{13}C (brown) between sites (Baie de l’Eau (BL), North Harbour (NH), and Swift Current (SC)), locations, and site and location combined. Patterns in spatial distribution were tested using generalised linear models with a beta distribution and a logit link for C_{org} and a gamma distribution with a log link function for C_{org} density, whereas a linear model using Gaussian distribution was used to detect spatial patterns in $\delta^{13}C_{org}$. Estimates are presented based on model link transformations (e.g., estimates for the C_{org} model are in logit scale). All model included transect ID as a random effect.

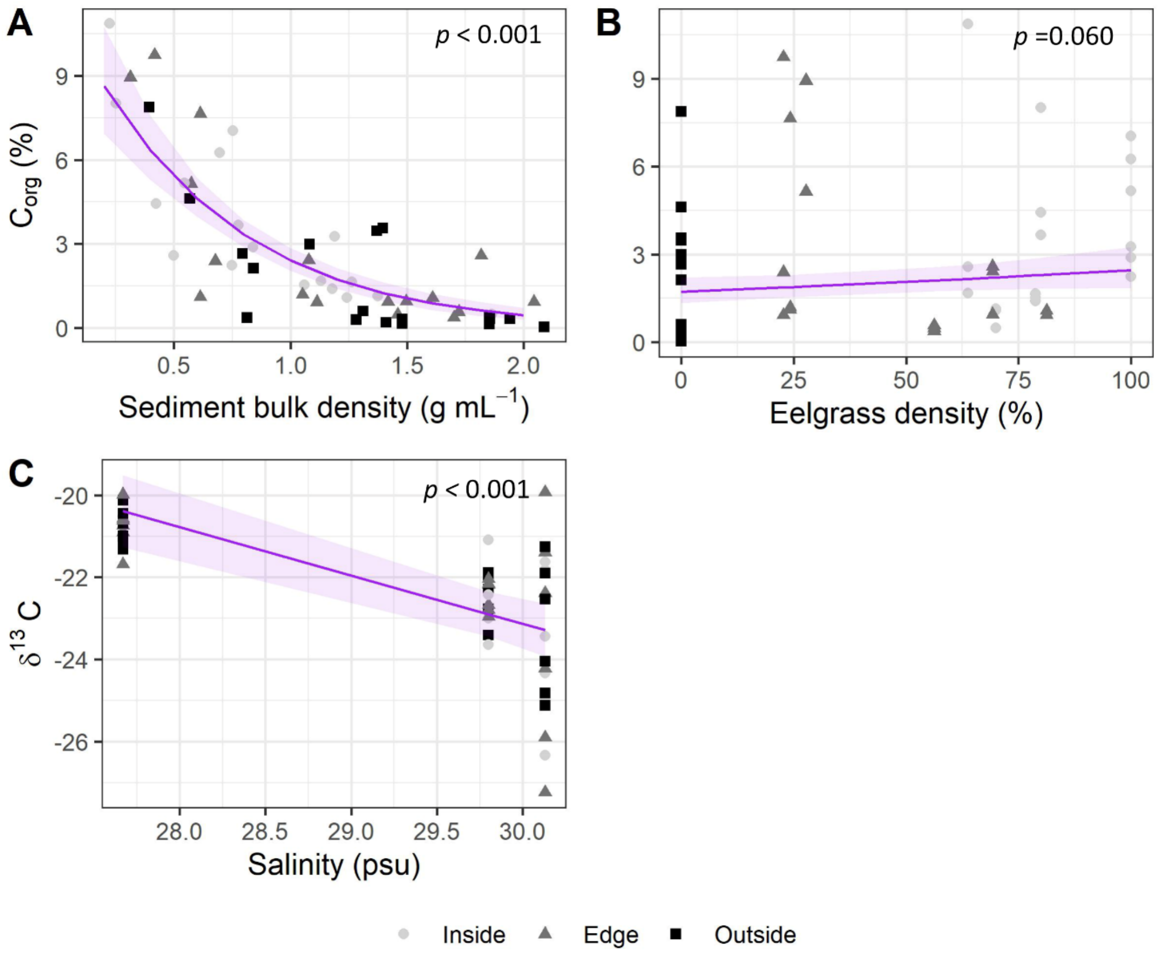

Figure 4.6: Relationship between carbon levels and sources against statistically significant environmental parameters according to models in Table S4.2. Shaded areas represent the 95% confidence intervals.

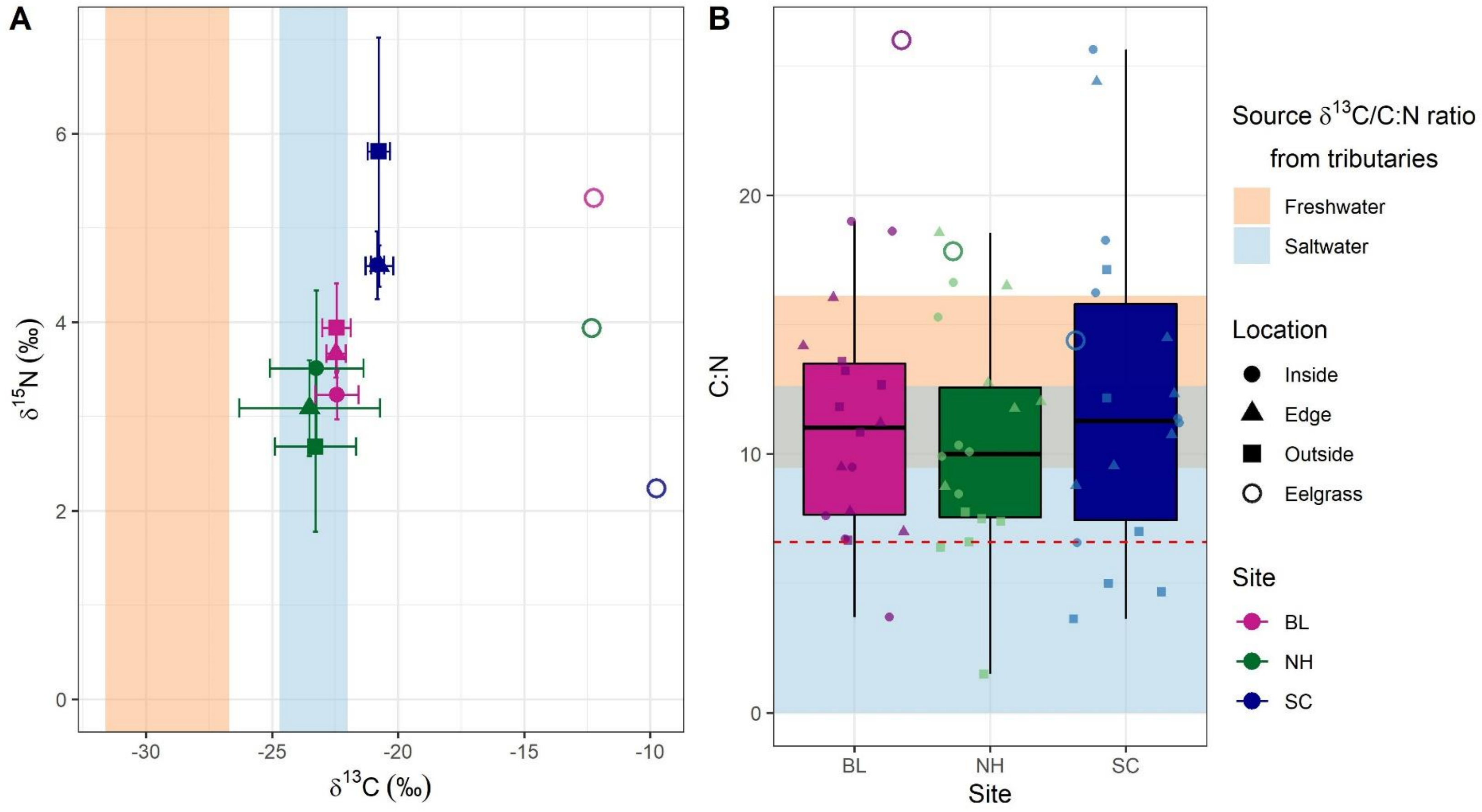

Figure 4.7: Biplot showing stable isotope values for each meadow by location (A) and boxplot showing the organic C:N ratio for each meadow by location (B). Source $\delta^{13}C_{org}$ values are according to Khoo *et al.* (2023), collected from Piper's Hole and Come by Chance. No $\delta^{15}N$ were available. Filled points represent data from sediment samples, hollow points represent data from eelgrass tissue samples, and grey shading in panel B is overlap between the source polygons. Red dashed line delineates the Redfield ratio for typical algae.

Chapter 5: Coastal community perceptions of eelgrass in Atlantic Canada: Considerations for management

5.1 Abstract

Societal awareness of the value of coastal ecosystems and the services they provide is necessary for public support of conservation and management decisions, yet public perception is seldom explored. I present findings from an online survey on coastal community perceptions of eelgrass (*Zostera marina*) and its management in Atlantic Canada and compare these findings with related scientific literature. Responses from 114 participants in an anonymous online survey indicate that people residing in coastal communities in Atlantic Canada are aware of the status of eelgrass meadows in their region, the services they provide, and threats to eelgrass meadows. Consistent with scientific literature, participants identified fish habitat (97%), coastal protection (93%), and water quality maintenance (89%) as the three most important eelgrass ecosystem services. Only 51% of participants selected climate change mitigation as a valuable eelgrass ecosystem service, consistent with its more recent appearance in scientific publications and the absence of Canadian policies on this service. Coastal development, climate change, and invasive species were identified as the most likely causes of change in eelgrass. More than 80% of participants indicated a need for increased restoration and protection, and 76% agreed that the public should be more involved in all aspects of eelgrass management. Although based on a non-random sample of the population, this study illustrates a relationship between scientific knowledge, public awareness, and existing Canadian

policies. Participants' knowledge of the societal benefits of eelgrass meadows and support for and interest in participating in the management process signals an opportunity to expand public engagement with eelgrass conservation efforts. This could begin by refining and introducing policies that protect the numerous ecosystem services eelgrass meadows provide.

5.2 Introduction

Cumulative anthropogenic impacts such as coastal development, exploitation, and run-off pollution have altered the status of coastal ecosystems and the provision of ecosystem services (i.e., direct and/or indirect benefits to people; Barbier et al. 2011) (Millennium Ecosystem Assessment 2005; Lotze et al. 2006; Halpern et al. 2008). Coastal habitats are decreasing globally (Duarte 2009; Waycott et al. 2009), and their resilience to increasingly frequent and severe disturbances has been reduced (Adger et al. 2005). Shifts in individual and societal actions and policies towards more sustainable practices and the development of management and conservation programs are necessary to mitigate the loss of coastal ecosystems (Millennium Ecosystem Assessment 2005; Cullen-Unsworth et al. 2014; Lotze et al. 2018). The likelihood of these shifts taking place relies on public support (Bennett 2016; Lotze et al. 2018; Unsworth et al. 2019a), which in turn may depend on public awareness of services obtained from coastal ecosystems and threats to these services, as public awareness of marine environmental issues often correlates with support for management and conservation actions (Steel et al. 2005a; Gelcich et al. 2014; Jefferson et al. 2015; Kelly et al. 2022). It is especially important to understand coastal inhabitant's awareness of coastal ecosystems as their frequent interactions and connection to these systems are most directly impacted by coastal ecosystem management decisions (Vincent 2011).

Seagrasses are valuable vegetated coastal habitats that often serve as ecosystem engineers and benefit humans by providing habitat for economically-important species (Nordlund et al. 2018b; Unsworth et al. 2018), sequestering carbon (Fourqurean et al. 2012;

Röhr et al. 2018), cycling nutrients (Schmidt et al. 2011), and stabilizing coastlines (James et al. 2019). The provision of these services varies among seagrass species and regions (Nordlund et al. 2016). Despite progress in the scientific understanding of the provision of ecosystem services by vegetated coastal ecosystems, public awareness remains limited (Unsworth et al. 2019a; McKinley et al. 2020). One reason for this is that research on coastal ecosystem services to date has been biased towards documenting ecological services, whereas social and economic services have been understudied (Ruiz-Frau et al. 2017; Heckwolf et al. 2021). While improving awareness of coastal ecosystems globally is critical for conservation of vegetated coastal habitats (Unsworth et al. 2019a), to effectively do this, we need to first understand how the public living near these ecosystems perceives coastal ecosystem services and how these perceptions differ from scientific knowledge.

Perception surveys can be used to understand how ecosystems are valued and to understand societal acceptability of conservation and management actions (Eddy et al. 2010; Benham 2017; Jefferson et al. 2021; Jones et al. 2022). Perceptions often vary within a community depending on experiences and social values (Glicken 2000; Jefferson et al. 2015; Bennett 2016). Communities may have regular resource users with multi-generational ecological knowledge of the local systems (e.g., fishers), such as knowledge of the system status, local threats, ecosystem services, and temporal changes (Bennett 2016). This knowledge can corroborate or be more accurate than knowledge gained by researchers who visit the system less frequently, with shorter time-series of observations, and can provide supplementary data for under-sampled areas. Alternatively, ineffective scientific knowledge dissemination may result in disagreements between scientists and communities regarding the status and importance of seagrass meadows and the ecosystem values they provide. Given the tightly coupled social-ecological nature of coastal systems, surveying regional variability in public perceptions of coastal ecosystems is key to identifying where awareness could be improved and to centering conservation and management actions around public interests, thereby increasing the likelihood of public support.

In an effort to assess the degree and effectiveness of mobilization of knowledge about coastal ecosystems and public support for management actions, this paper presents findings from an anonymous online survey of coastal community perceptions of eelgrass (*Zostera marina*) in Atlantic Canada. Eelgrass is the dominant seagrass species along the Northwest Atlantic coastline and it is widely distributed across the eastern Canadian coastline (DFO 2009). Eelgrass meadows host numerous vertebrate and invertebrate species, and serve as a preferred nursery habitat for commercially and culturally important fish species such as Atlantic cod (*Gadus morhua*) (Laurel et al. 2003b). The Canadian government has designated eelgrass in eastern Canada as an *ecologically significant species* in recognition that perturbation of eelgrass habitat results in substantially greater negative ecological consequences than equal perturbations on other species (DFO 2009). As a result, substantial efforts and resources are being invested to map eelgrass distribution across the country (e.g., National Eelgrass Task Force; Gomez et al. 2021), restore eelgrass meadows (e.g., Coastal Restoration Fund and Aquatic Ecosystems Restoration Fund), and better understand and quantify eelgrass ecosystem services including eelgrass contribution as a blue carbon ecosystem (Kelly et al. 2023). Furthermore, Murphy *et al.* (2021) recently published a synthesis of scientific knowledge on eelgrass ecology and management across

Canada, including an analysis of regional commonalities and differences in eelgrass status and causes of change. The current momentum around eelgrass research and management in eastern Canada presents an ideal opportunity to assess public perceptions of eelgrass in the region, to compare these perceptions with scientific literature, and ultimately to facilitate the integration of perceptions of coastal community members into coastal and ocean management policies in Canada. By focusing on people living in Canadian Atlantic coastal communities, where the effects of coastal change and management measures are more direct, this chapter had three main objectives:

1. to evaluate coastal community perceptions of eelgrass status, causes of change, and ecosystem services in Atlantic Canada, and determine whether these perceptions vary regionally;
2. to compare coastal community perceptions of eelgrass ecosystem services with publication trends in the scientific literature to identify potential pathways of knowledge mobilization; and
3. to describe coastal community perceptions of current eelgrass management in Atlantic Canada.

5.3 Methods

5.3.1 Survey

I distributed an anonymous online survey using Qualtrics© software to the public living in the four Canadian Atlantic provinces, namely Nova Scotia (NS), New Brunswick (NB), Prince Edward Island (PEI), and Newfoundland and Labrador (NL), encompassing three marine bioregions, namely the Newfoundland and Labrador Shelves, the Scotian Shelf, and the Gulf of St. Lawrence. I restricted the survey to public living in Canadian Atlantic provinces because eelgrass status as an ecologically significant species originates from Atlantic Canada (DFO 2009). Participation was also restricted to individuals with a house or a cottage within 50 km from the coast to capture the eelgrass perceptions of people that are more likely to have observed changes in eelgrass meadows and to be more directly affected by them. The questionnaire consisted of 39 questions divided into four sections: observations and experience with eelgrass meadows; valuing eelgrass meadows; management of eelgrass meadows; and participant's background (see Appendix D for questionnaire). I advertised the survey via a variety of media (e.g., Canadian Broadcasting Corporation radio) and social media (e.g., Facebook, Twitter) platforms. I also contacted recreational and working groups, including outdoor societies, and government, non-profit, and academic organizations in the region and asked them to distribute information about the survey to members and via their websites and email lists. Access to the questionnaire remained open for one year (August 2020-2021). Participation was anonymous and voluntary. None of the questions were mandatory for participants to answer. Participants could not revisit their responses after submitting the survey. After closing access to the questionnaire, I analyzed the responses using descriptive statistics (i.e., proportions and counts) in R (v. 1.2.5033; R Core Team 2019). Questionnaire design, recruitment, and consent were approved by Memorial University's Interdisciplinary Committee on Ethics in Human Research (ICEHR, file# 20204569).

5.3.2 Comparing public perceptions of eelgrass ecosystem services with scientific knowledge

I assessed the consistency between coastal community perceptions and scientific knowledge by comparing participant perceptions of eelgrass ecosystem services to the cumulative number of scientific papers published per year on each ecosystem service in Canada. Specifically, I used Web of Science to search for studies on eelgrass ecosystem services in Canada up to and including 2022 (when the literature review was conducted). I restricted the literature search by specifying the following search terms in each query: “Canada” AND either “eelgrass”, “seagrass”, or “*Zostera marina*”, AND an ecosystem service (see Appendix B for the list of ecosystem service terms searched). I reviewed titles, abstracts, and results to confirm that each paper focused on studying eelgrass ecosystems services in Canada and excluded papers where the ecosystem service was not part of the study focus (e.g., ecosystem service only briefly mentioned in the introduction). If a paper included more than one ecosystem service in the analyses, the paper was included in the publication tally for each service. The literature search yielded 81 relevant papers, and 112 publication counts after accounting for studies that included more than one ecosystem service in their scope (see Appendix E for a list of relevant papers and associated ecosystem services). To assess the consistency between scientific knowledge and coastal community perception, I compared the cumulative number of papers published discussing each eelgrass ecosystem service to the participant responses to the survey questions on eelgrass ecosystem services (i.e., survey part 2. valuing eelgrass meadows).

5.4 Results

5.4.1 Participant background

I collected 116 survey responses from participants evenly spread across all age classes from 19 to 80+ years old (Figure 5.1). One participant resided farther than 50 km from the coast and one participant did not specify their province of residence; both were therefore excluded from the analyses (Figure S5.1). Of the remaining 114 participants, most resided in NS (59%) or NL (30% from Newfoundland and none from Labrador). Only 11% of the participants were from PEI (7 participants) and NB (6 participants) (Figure 5.1). To assess regional differences in coastal community perceptions, participants were grouped into one of three marine bioregions based on their county of residence (i.e., Scotian Shelf, Gulf of St. Lawrence, or the Newfoundland and Labrador Shelves). One participant did not specify their county of residence, reducing the bioregional comparisons' sample size to 113 participants. Fifty percent of participants resided in the Scotian Shelf bioregion, 23% resided along the Gulf of St. Lawrence, and 27% resided along the Newfoundland and Labrador Shelves. I also explored regional differences across provinces, namely NS and NL due to small sample size in the other provinces, and the Maritimes (71%; grouping NB, NS, and PEI) versus NL (29%), both of which yielded similar findings as the bioregional comparisons presented in this study. Additionally, all except for one participant (omitted 10 questions) responded to all of the questions in the questionnaire, and 7 participants ranked the ecosystem services (Appendix D question 11) incorrectly by attributing the same rank to more than one service. In these cases, percentages were calculated according to the total number of correctly completed responses.

Although all individuals with residences or cottages within 50 km of the coast were eligible to participate, 60% of participants lived <1 km from the coast (Figure S5.1), and 62% frequented the coast year-round (Figure 5.1). Seventy-nine percent of respondents had observed eelgrass within 50 km of where they reside. Respondents reported using the Canadian Atlantic coastline for numerous activities, particularly walking, hiking, or boating (Figure 5.2). While most participants did not work outdoors near coastal habitats (57%), suggesting that the majority of the participants used the coast recreationally (Figure 5.1), a large proportion (45%) of respondents had a professional relationship with the environment. Specifically, 2.6% of participants taught environmental education, 10.5% worked in an environmental conservation field, 0.9% fished commercially, 24.6% worked in environmental conservation and taught environmental education, 4.4% worked in environmental conservation and fished commercially, and 1.8% did all three. This suggests that the sampled population is skewed toward those living close to or on the coast, with high levels of engagement with the coast, and towards a higher proportion of individuals with a professional relationship with the coast and greater interest in environmental issues compared to the larger coastal population in the four Atlantic provinces.

5.4.2 Part 1 – Eelgrass status and causes of change

The first part of the survey inquired about coastal community perceptions of changes and causes of change in eelgrass meadows. Most participants had observed eelgrass (Figure 5.3A, B), and 50% indicated that the size and number of eelgrass meadows had decreased in their region; 10% indicated that no change had occurred, and 13% indicated that eelgrass meadows had increased (Figure 5.3C). A higher percentage of participants along the Scotian Shelf (57%) and the Gulf of St. Lawrence (50%) than in the Newfoundland and Labrador Shelves bioregion (37%) indicated that the number and size of eelgrass meadows had decreased in their region. In contrast, a higher percentage of participants along the Newfoundland and Labrador Shelves (27%) compared to the Gulf of St. Lawrence (19%) and the Scotian Shelf (4%) indicated that the number and size of eelgrass meadows increased in their region (Figure 5.3D). Of the participants that indicated eelgrass was increasing in the Gulf of St. Lawrence, none resided in NL. Interestingly, only participants from the Scotian Shelf and the Gulf of St. Lawrence bioregions indicated that the shoreline had changed a lot (27% and 15%, respectively; 0% from Newfoundland and Labrador Shelves bioregion). This corresponded with survey responses indicating a decline in eelgrass status, particularly in the Scotian Shelf bioregion.

Participants were asked to select the causes of change in eelgrass meadows from a list provided and to rank, in their opinion, the top three causes of changes. Participants identified invasive species, coastal development, and climate change as the three main causes of change in eelgrass in Atlantic Canada (Figure 5.4). However, some variability was observed depending on participants' professional background. Specifically, 65% of respondents who had worked in environmental conservation selected invasive species as a threat to eelgrass meadows, whereas only 24% of the participants who did not work in environmental conservation indicated invasive species as a threat (Table 5.1). Perceptions of causes of change in eelgrass meadows also varied regionally with participants from the Gulf of St. Lawrence and the Scotian Shelf bioregions identifying aquaculture (23% and 34%, respectively) and agriculture runoff (31% and 29%, respectively) as causes of changes in eelgrass meadows, whereas neither of these causes was selected by participants residing in the Newfoundland and Labrador Shelves bioregion (3% for agriculture runoff; 0% for aquaculture). Instead, 20% of participants from the Newfoundland and Labrador Shelves identified boat scouring as a cause of change. Additional regional differences included a greater proportion of participants from the Newfoundland and Labrador Shelves selecting coastal development and invasive species as causes of change over climate change (10% and 17% higher, respectively), whereas climate change was perceived as having the same impact as coastal development and invasive species according to participants residing in the Scotian Shelf bioregion (only ≤7% difference, Figure 5.4B; Table 5.1), and the greatest impact in the Gulf or St. Lawrence (7% higher than invasive species and 22% higher than coastal development). Finally, when prompted to list additional causes of change, almost all participants explicitly stated or alluded to human activities particularly nutrient loading activities such as pollution, dredging, runoff, and eutrophication (many of these were different terms for causes of change already included in the options listed in the survey).

5.4.3 Part 2 – Perceptions of eelgrass ecosystem services

The second section of the survey assessed participants' perceptions of the ecosystem services provided by eelgrass meadows. Overall, the five top ranked ecosystem services were fish habitat (97%), coastal protection (93%), water quality maintenance (89%), animal habitat other than fish (73%) and climate change mitigation (51%) (Figure 5.5). Fish habitat was ranked in the top two positions more often than other ecosystem services, indicating that the coastal communities perceived eelgrass predominantly as a fish habitat. This result was generally consistent across participant age groups (Figure S5.2) and participant job and fishing background (Figure S5.3), and bioregions (Figure S5.4). Furthermore, it was consistent with the literature review of scientific publications on eelgrass ecosystem services in Canada, which showed that fish habitat is the most and longest studied eelgrass ecosystem service (Figure 5.6). Similarly, >25% of the participants indicated food security among the top five ecosystem services provided by eelgrass (Figure 5.5). In contrast, findings from research on the role of eelgrass in water quality maintenance, coastal protection, and as vertebrate habitat have been published more recently, mostly in the last 10 years.

Our literature review also revealed that carbon sequestration is the third most studied ecosystem service provided by eelgrass in Canada, but with most publications occurring in the last five years (Figure 5.6). In contrast, only 51% of survey participants selected climate change mitigation as a valuable ecosystem service provided by eelgrass meadows (Figure 5.5). This number was higher for participants who work(ed) in environmental conservation (62%) than those who did not (46%), but was fairly consistent across bioregions (51% from the Scotian Shelf, 47% from the Gulf of St. Lawrence, and 46% from the Newfoundland and Labrador Shelves). Finally, while the literature review did not yield any studies on the direct use of eelgrass by coastal communities in Atlantic Canada, survey responses show that 17% of participants attributed eelgrass serving as mulch and agricultural fertilizer and one participant commented that eelgrass is still used on the eastern shore of NS as insulation around the foundation of houses.

5.4.4. Part 3 – Management of eelgrass and public involvement

The third section of the survey assessed participants' perceptions of eelgrass management in Atlantic Canada. More than 80% of participants indicated that the federal and provincial governments should invest more in the protection of eelgrass meadows in Atlantic Canada (Figure 5.7A). However, there was also a clear perception that payment for the protection or restoration of eelgrass should involve a partnership between different sectors, as indicated by 75% of participants. Specifically, 34% of participants indicated it should be subsidized by both industry and government sectors, whereas 33% indicated communities should contribute as well. These results were consistent across bioregions, age groups, and whether participants worked in environmental conservation or were fishers (Figure S5.5). Where participants identified other groups that should contribute to paying for eelgrass protection or restoration, two participants indicated non-profit organizations and five participants added the party deemed responsible for the destruction should be required to pay for the protection/restoration.

The three most popular management actions among participants included controlling development in coastal regions (93%), controlling the spread of invasive species (83%), and improving wastewater treatment (74%). Survey responses addressing questions on eelgrass restoration indicated that 81% of respondents favour restoration efforts focusing on eelgrass meadows that are decreasing in size and 47% selected focusing restoration efforts on meadows that have disappeared (participants were allowed to select more than one option). Additionally, 29% of participants favoured restoration targets for eelgrass meadows that are in remote locations and 43% favoured meadows near communities. Sixteen percent of participants indicated they did not know what restoration involves and 2% of participants indicated restoration is not an effective management approach. Lastly, in addition to supporting conservation of eelgrass, >90% of participants indicated the public should be more involved in all steps of management and protection/restoration of eelgrass, including planning, implementing regulations, and monitoring (Figure 5.7B, C). This opinion was consistent across bioregions, age groups, and occupation (Figure S5.6).

5.5 Discussion

A barrier to incorporating public perception into ocean conservation and management is the limited effort by experts to understand the awareness and perceptions of coastal ecosystem users (Gelcich et al. 2014; Potts et al. 2016). Within the growing field of ocean perception research (Jefferson et al. 2021), several studies have suggested there is limited public awareness of marine environmental issues (Fletcher et al. 2009; Potts et al. 2016; Lotze et al. 2018), including the benefits of vegetated coastal ecosystems such as saltmarshes (McKinley et al. 2020) or seagrass meadows (Unsworth et al. 2019a). Differences between public perception and scientific knowledge of the ocean vary according to respondent background, such as variability between countries, age groups, and types and degree of interactions with the ocean (Lotze et al. 2018; Jefferson et al. 2021). People residing near the coast are more likely to have unique perceptions due to their frequent interactions with coastal ecosystems and may be directly affected by coastal management actions (Vincent 2011). My anonymous survey sought to assess the perceptions of eelgrass by people residing in coastal communities living in Canadian Atlantic provinces, within 50 km from the coast, and of mixed ages and occupational backgrounds. Keeping in mind that the resulting sample of respondents was skewed towards individuals living near the coast and likely a higher proportion of individuals interested in environmental issues compared to the larger population living in Atlantic Canada, their responses reveal that the perceptions of eelgrass ecosystems by this sample closely match findings and concerns highlighted in related scientific research, regardless of participant background (i.e., age, bioregion of residence, occupation). Specifically, by drawing parallels between participant survey responses and scientific knowledge, my findings indicate that within this sample of the public there is strong but variable awareness of eelgrass ecosystem services, threats to eelgrass meadows, and overall concern about the impact eelgrass loss may have on fish and coastal areas.

5.5.1 Perceptions of eelgrass status and causes of change

The total extent of eelgrass in Canada is unknown due to limited maps, and few eelgrass meadows have sufficient data to assess temporal changes in biomass, extent, or shoot density limiting the capacity to comprehensively assess eelgrass status in Canada (Garbary and Munro 2004; Murphy et al. 2021). Using data from Environment and Climate Change Canada, Murphy et al. (2021) reported that 31% of eelgrass meadows are declining in Atlantic Canada, but with marked differences across bioregions. For instance, in the Scotian Shelf bioregion, 50% of eelgrass meadows are decreasing and the rest are stable. Similarly, in the Gulf of St. Lawrence bioregion, ~60% of eelgrass meadows are decreasing, ~15% are stable, and ~25% are increasing. Meanwhile, in the Newfoundland and Labrador Shelves bioregion, ~45% of eelgrass meadows are increasing, ~50% are stable, and only ~5% are decreasing presumably due to the introduction of invasive green crab (*Carcinus maenas*) (Matheson et al. 2016). These regional trends are only partially consistent with the survey results. A majority of participants from the Scotian Shelf (57%) and half of the participants from the Gulf of St. Lawrence indicated eelgrass meadows were decreasing, consistent with findings from Murphy et al. (2021). In contrast, a large portion of participants from the Newfoundland and Labrador Shelves (28%) indicated eelgrass meadows were decreasing, despite Murphy et al. (2021) indicating eelgrass meadows to be primarily increasing or stable. Similarities between the survey results and the synthesis by Murphy et al. (2021) show that the surveyed members of coastal communities are generally aware of trends in eelgrass meadows and supports the growing idea that such members of the public, through various citizen science projects, could provide a valuable option to monitor coastal habitats such as eelgrass meadows (Jones et al. 2018; Dalby et al. 2021). However, differences between the survey responses and Murphy et al. (2021) findings, along with the relatively high portion of participants that indicated they did not know the status of their local eelgrass meadows (27%), highlights a need to continue mobilizing knowledge on the status of eelgrass in Atlantic Canada.

Understanding the causes of degradation, how they vary across regions, and whether the public is aware of these causes are necessary to develop and ensure public support for effective eelgrass conservation measures. Survey findings indicate that, for this sample, coastal community perceptions of the causes of changes to eelgrass status generally agreed with the scientific literature as coastal development, invasive species, and climate change were identified as three of the main causes in both the survey responses and in the scientific literature (Matheson et al. 2016; Murphy et al. 2019, 2021). However, invasive species was predominantly perceived as a cause of change by participants who worked in environmental conservation. Reasons for this could be that respondents who did not work in environmental conservation were more likely to be unfamiliar with which species are invasive, or that they have not observed invasive species in their local eelgrass habitats. Damage to eelgrass meadows by invasive species such as European green crab (*Carcinus maenas*) and golden star tunicate *(Botryllus schlosseri*) has been well documented across Atlantic Canada (Malyshev and Quijón 2011; Wong and Vercaemer 2012; Matheson et al. 2016). Given that the spread of invasive species is often facilitated by human activity (e.g., release of ballast water by ships, failure to clean equipment when moving between sites), more education on invasive species may benefit eelgrass conservation.

Causes of change to eelgrass meadows vary regionally, and such variability was apparent in participant responses. For instance, while eelgrass decline in NL (Placentia Bay) has been attributed to the invasion of European green crab (Matheson et al. 2016), run-off pollution associated with human activities such as agriculture land-use, municipal sewage, and aquaculture have been documented as primary threats to eelgrass in PEI, NS, and NB (Murphy et al. 2019, 2021; Grizard 2013 [run-off from potato farms in PEI]; McIver et al. 2015, 2019 [run-off from peat mining in NB]). Consistent with these regional studies, aquaculture and agriculture runoff were mostly only recognized by participants from the Scotian Shelf and the Gulf of St. Lawrence bioregions, whereas participants from the Newfoundland and Labrador Shelves bioregion identified boat scouring as a higher cause of change compared to other causes. Agriculture and aquaculture activities in NL are currently less widespread compared to other Atlantic provinces, likely partially explaining these perceived regional differences.

5.5.2 Perceptions of eelgrass ecosystem services

Fish habitat is the most and longest studied ecosystem service provided by eelgrass in Atlantic Canada, and it was also deemed the most important by respondents. The role of eelgrass as an important nursery habitat for juvenile Atlantic cod, an iconic fish species in Atlantic Canada, has long been recognized in the scientific literature (Gotceitas et al. 1997; Lilley and Unsworth 2014) and this knowledge has been widely disseminated. Accordingly, the predominant Canadian legislation that protects eelgrass is the Fisheries Act, with the No Net Loss policy focusing on protecting fish habitat (Howarth and Reid 2021; Murphy et al. 2021). Water quality maintenance and coastal protection are two services that have also been relatively well studied. Both were identified among the three most important services by the surveyed population, and are linked to existing provincial policies such as the Nova Scotia's water resource management strategy (Government of Nova Scotia 2010) and the proposed Coastal Protection Act (Province of Nova Scotia 2022). These examples of shared recognition of important eelgrass ecosystem services demonstrate successful mobilization of scientific knowledge raising public awareness and translation of this knowledge into policy.

While carbon sequestration is currently the third most studied ecosystem service in Atlantic Canada, it has only been extensively studied in the last five years. A majority of survey respondents ranked it as the fifth most important ecosystem service and there are currently no policies directed towards protecting eelgrass meadows as carbon stocks (East Coast Environmental Law 2022). This may reflect a gap or delay in knowledge mobilization of the role of eelgrass as blue carbon ecosystems or possibly a lack of consensus in the scientific literature on the importance of eelgrass as a blue carbon ecosystem in temperate regions as revealed by recent studies in Canada (Postlethwaite et al. 2018; Chapter 4). Limited public awareness of the contribution of seagrass as a carbon sink was also reported in a recent case study in Australia (Losciale et al. 2022), supporting the hypothesis that there is a gap in knowledge mobilization. While there is an opportunity for further knowledge mobilization on the contribution of eelgrass to climate change mitigation, overall consistency between survey responses on the importance of various eelgrass ecosystem services and trends in the published scientific literature reveals that this segment of the Canadian Atlantic public is aware of the direct and indirect social, ecological, and economic benefits that eelgrass meadows provide. This awareness points to an opportunity for management to identify and evaluate policy actions centered around conserving eelgrass ecosystem services as there is likely coastal community support to preserve these services.

5.5.3 Management

In addition to showing that the sampled population is generally aware of eelgrass ecosystem services, the survey indicated coastal community support for more eelgrass conservation effort moving forward, particularly protection and restoration. Previous public perception research has shown there is global public support for more ocean protection (Lotze et al. 2018). Various management actions are ongoing in Atlantic Canada to mitigate the impacts of human activities on coastal vegetated ecosystems. For instance, Nova Scotia implemented a water resource management strategy in 2010 (Government of Nova Scotia 2010) and recently proposed a new Coastal Protection Act (Province of Nova Scotia 2022). Similarly, the Canadian Fisheries Act of August 2019 reinforced the protection of fish habitat, and as part of the National Ocean Protection Plan (DFO 2020; Government of Canada 2021), efforts are ongoing to restore degraded marine ecosystems including eelgrass meadows in several Canadian provinces. My study indicated that people living in Canadian Atlantic coastal communities are interested in being more involved in all steps of management of coastal habitat, suggesting that the current momentum for the protection of coastal vegetated habitat could be strengthened by further including the public in mitigation actions and management plans.

In Canada, management of coastal ecosystems is divided between government sectors, where habitats (including eelgrass meadows) below the low-tide mark are managed federally (i.e., Fisheries and Oceans Canada), and habitats above the low-tide mark are managed at the provincial/territorial and municipal levels. My survey indicated people living in coastal communities favour management actions that involve a partnership between federal and the provincial governments, industry, and communities. Although, five participants indicated the party responsible for the destruction of eelgrass should be held accountable for paying for management actions, this may not be feasible if the eelgrass is being affected by large scale threats where there is no specific party that is culpable or identifiable, as in the case of invasive species.

5.5.4 Study limitations

This study presents findings from an exploratory online survey with a small number of respondents (114) relative to the larger coastal Atlantic population. Online surveys have well-known weaknesses rendering them prone to coverage error and non-response error (Vaske 2008). For instance, online surveys are restricted to individuals with internet, it is difficult to assess whether participants understood each question, and the sampled population may not include all the perceptions in the population of interest. This means the findings from this study cannot be generalized to the broader population. Responses also depended on participants volunteering to complete the questionnaire, biasing study respondents towards those interested in eelgrass or similar habitats, and those with environmental concerns and knowledge. Specifically, 45% of participants had a professional relationship with the environment (i.e., commercial fisher, taught environmental education, or worked in environmental conservation) leaving me to expect that the remaining 55% represent members of the general public that do not have knowledge of eelgrass coastal ecosystems because of their job. These proportions are unlikely to represent the true composition of the broader coastal population, and those who are unaware of what eelgrass does or who lack an active interest in coastal habitats are likely underrepresented among respondents. The 'snowball' method used to distribute the survey, where participants were encouraged to share the survey with their contacts, and information about the survey may have contributed to this bias, although the survey was also more widely available through media and social media platforms, and available for a long period of time. Coastal community perceptions captured here cannot be generalized to the wider Canadian public as these may differ between those living in coastal and non-coastal regions (Steel et al. 2005b). However, it is important that the perceptions of the public whose livelihoods depend on the ecosystem services and who are potentially affected by management decisions be known. “Go where the users are” is one way knowledge mobilization and knowledge exchanges can be improved between experts and non-experts (Young et al. 2016), especially for issues where biological richness and human uses overlap most (Vincent 2011). This may explain the enhanced awareness of eelgrass observed in the current study compared to previous public perception research (Jefferson et al. 2014; Unsworth et al. 2019a; McKinley et al. 2020) since I surveyed individuals living near the coast and with a high proportion of individuals interested in environmental issues compared to broader populations.

5.5.5 Conclusion

Expanding eelgrass conservation could begin by refining and introducing policies that protect the different ecosystem services provided by eelgrass and other coastal ecosystems. This study illustrates that mobilization of scientific knowledge of eelgrass ecosystems services relates to raised coastal community awareness and may contribute to successful translation into Canadian policy. Recognizing this relationship between scientific knowledge, public awareness, and policy is the first step towards identifying where protection may be lacking, and where policies and management plans could be implemented. Similarities in eelgrass perceptions between scientists and the public living along the Canadian Atlantic coast suggest that residents of coastal communities could monitor coastal habitats such as eelgrass meadows through citizen science and help to identify threats. Additionally, these similarities might also exist for other communities living along the coast and with respect to other ecosystems. Therefore, surveys of coastal community perceptions across different bioregions, demographics, and different ecosystems are warranted. Interacting with resource users connects experts to the relevant socio-ecological dependencies and exposes knowledge mobilization pathways and gaps. These interactions could help ensure development and communication of management actions around issues that the public cares about and by promoting public awareness, could increase support for those actions. Furthermore, my results demonstrated that survey participants share strong support for management of eelgrass in Atlantic Canada, exposing an opportunity to expand eelgrass conservation in the region.

Table 5.1: Relationship between participant background and their perception of the top five causes of change to eelgrass in Atlantic Canada. Numbers indicate the number of participants who selected or did not select the cause.

Drivers of observed change in eelgrass	**Bioregion**						**Worked in environmental conservation**				**Fish**			
	Scotian Shelf		Newfoundland and Labrador Shelves		Gulf of St. Lawrence		Yes		No		Yes		No	
Selected (yes/no)	*yes*	*no*	*yes*	*no*	*yes*	*no*	*yes*	*no*	*yes*	*no*	*yes*	*no*	*yes*	*no*
Invasive species	24	33	12	18	12	14	31	17	16	50	28	20	25	41
Coastal development	27	30	14	16	8	18	21	26	25	42	26	27	25	36
Climate change	23	34	9	21	14	12	24	23	22	45	24	23	22	45
Agricultural runoff	19	38	1	29	6	20	15	32	11	56	12	41	14	47
Aquaculture	16	41	0	30	8	18	10	37	14	53	7	46	17	44

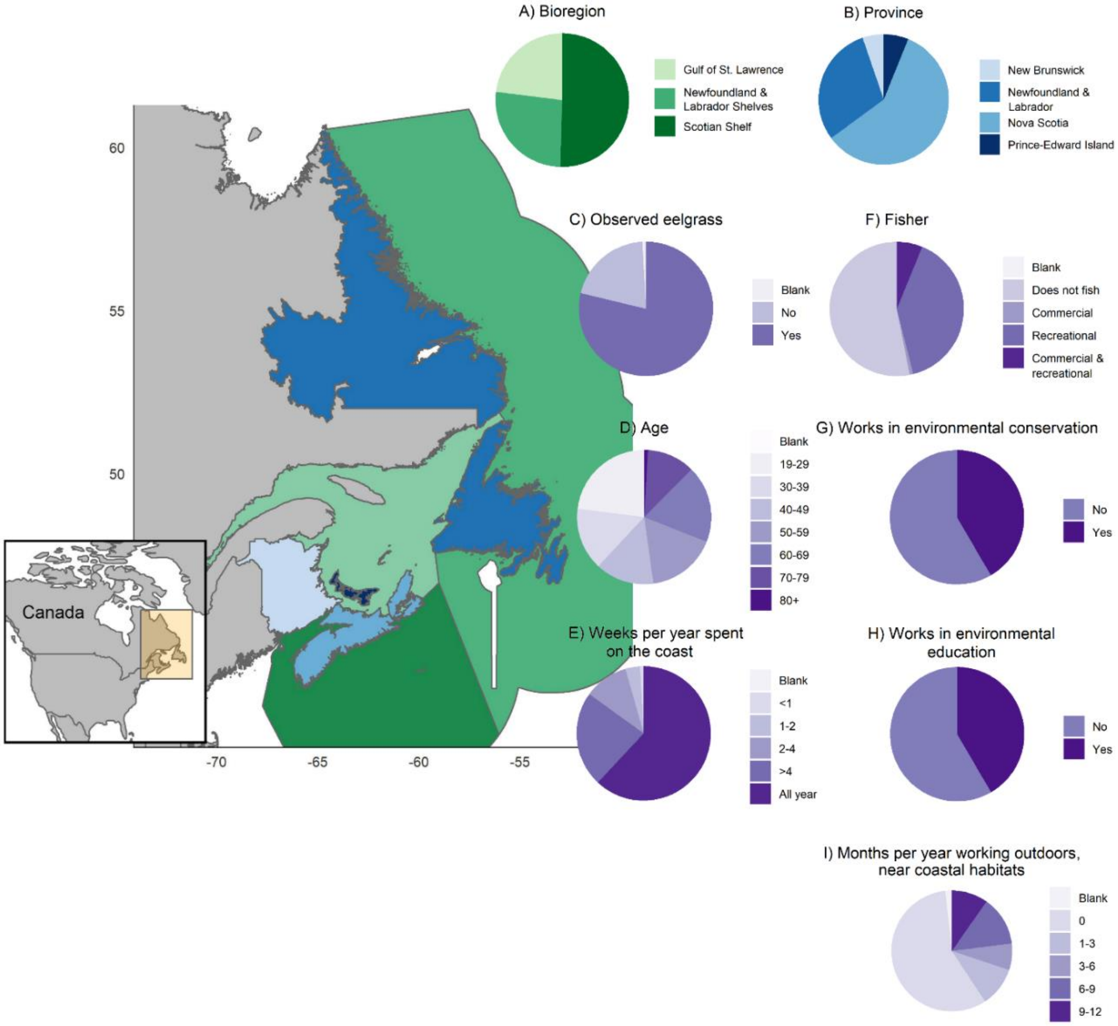

Figure 5.1: Survey participant background including: A) Bioregion of residence, B) province of residence; C) whether participant has observed eelgrass; D) age; E) number of weeks per year participant spends along the coast; whether participant F) fishes; G) works in environmental conservation; H) works in environmental education; and I) the number of months per year participant works outdoors near the coast. White area delineates area outside the surveyed bioregions.

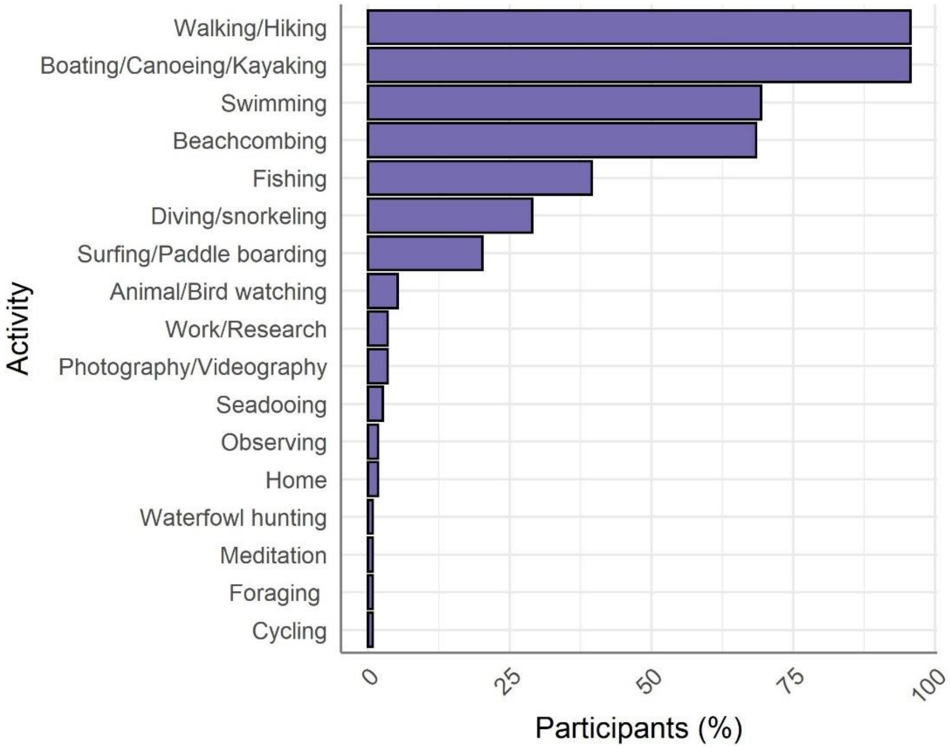

Figure 5.2: How survey participants spend time on the coast in Atlantic Canada. Percentage was calculated out of the 114 participants.

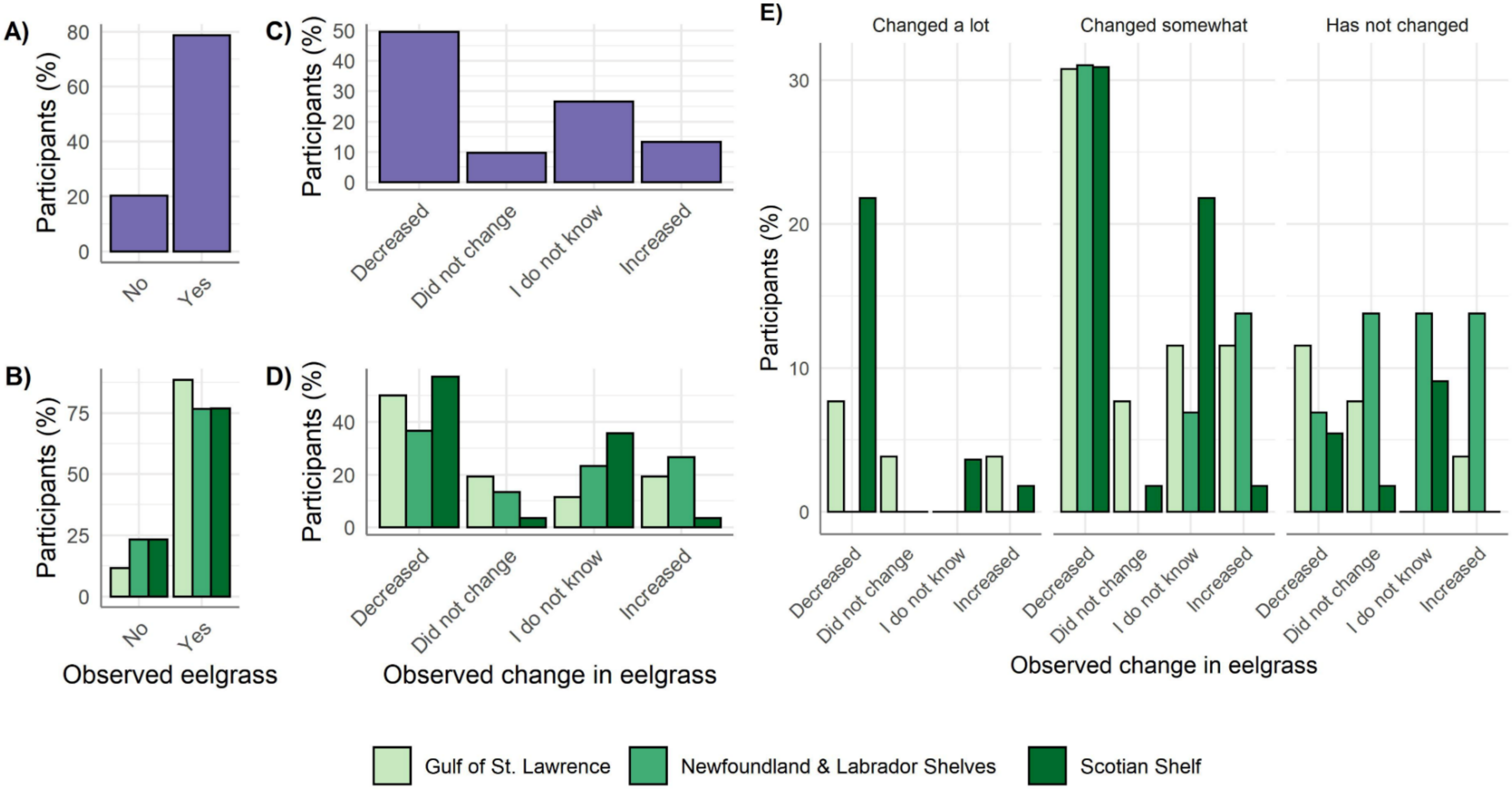

Figure 5.3: Proportion of participants who have observed eelgrass within 50 km of their residence across Atlantic Canada (A, B, n=113 participants), and across bioregions including the Gulf of St. Lawrence (n=26), the Newfoundland and Labrador Shelves (n=30), and the Scotian Shelf (n=57) bioregions (C, D), and the observed change in eelgrass according to the perceived change in the surrounding coastline (i.e., coastline changed a lot, somewhat, no change) in each bioregion (E).

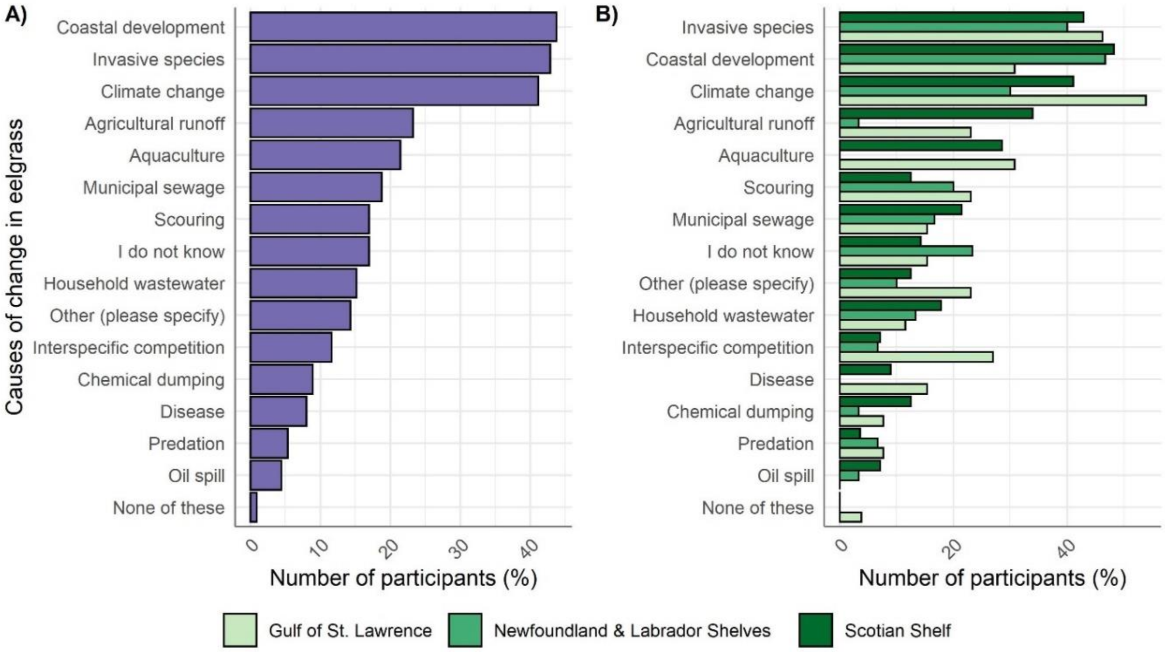

Figure 5.4: Causes of change in eelgrass meadows according to participants from Atlantic Canada (A, n=113) resident in the Gulf of St. Lawrence bioregion (n=26), the Newfoundland and Labrador Shelves bioregion (n=30), and the Scotian Shelf bioregion (n=57) (B).

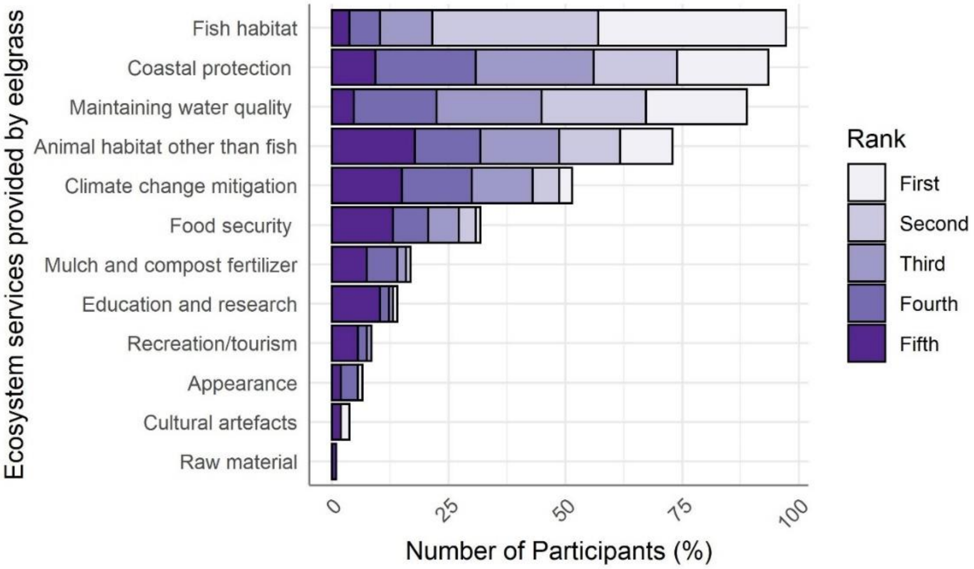

Figure 5.5: Ranking by survey participants (n=107) of the top 5 ecosystem services provided by eelgrass meadows.

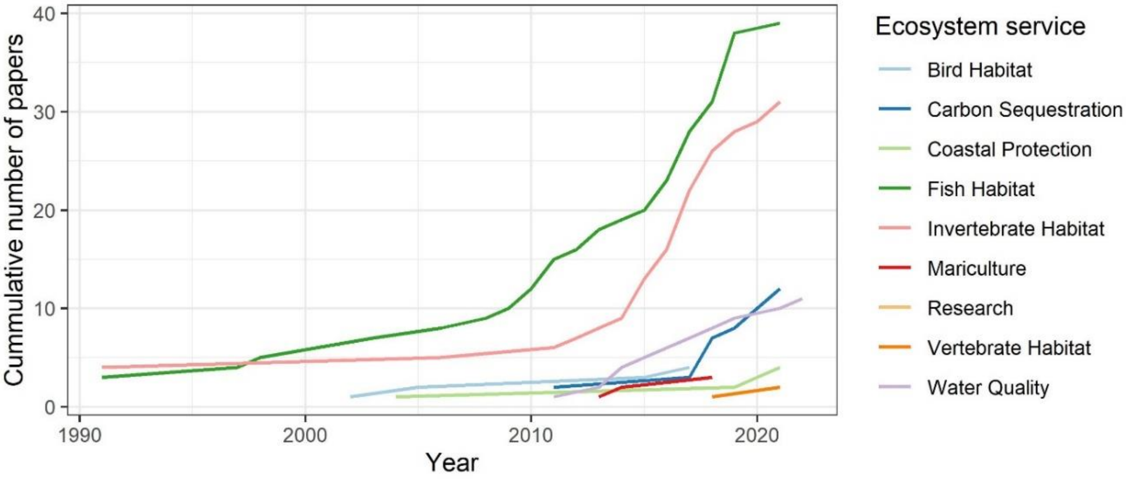

Figure 5.6: Cumulative sum of the number of papers published on the Web of Science discussing the provision of ecosystem services by eelgrass meadows in Canada. Colours represent the different ecosystem services.

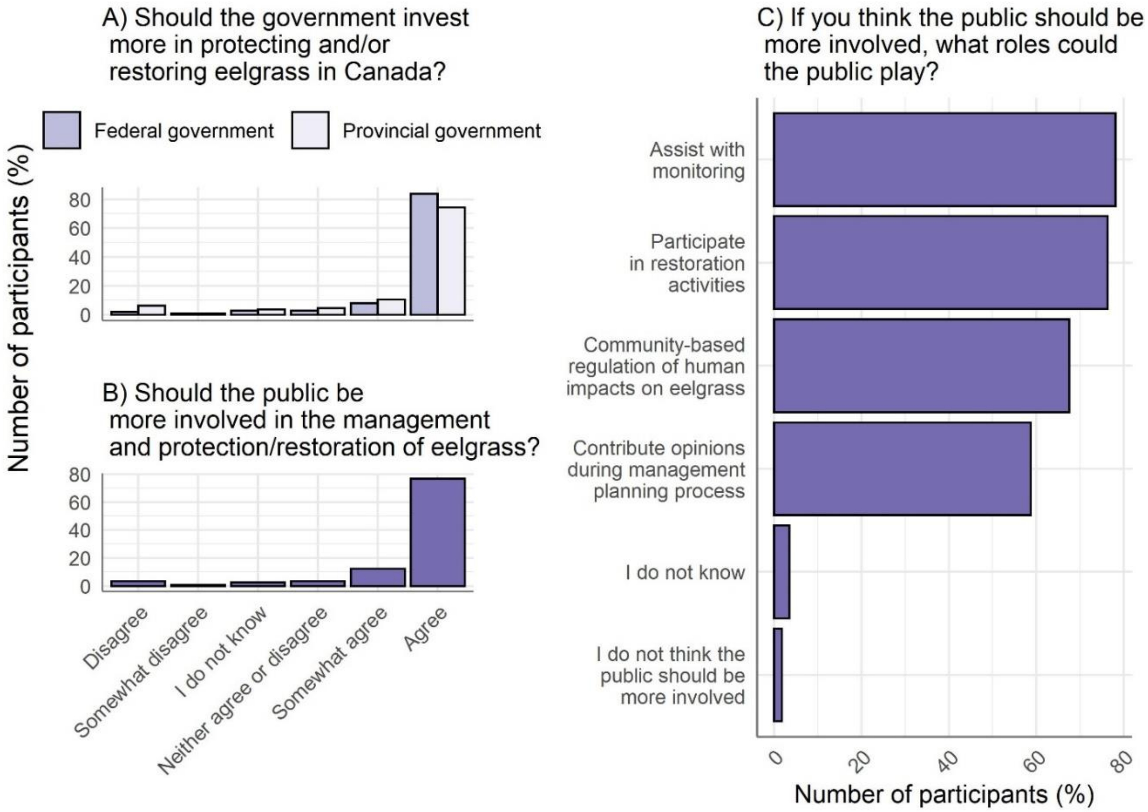

Figure 5.7: Public perception (n=114 participants) of who should manage and pay for the protection and/or restoration of eelgrass meadows in Atlantic Canada (A), whether the public should be involved in management (B), and ways that the public should be more involved in eelgrass management (C).

Chapter 6: Synthesis

There is no doubt that seagrass meadows worldwide are affected by environmental and anthropogenic disturbances (Lotze et al. 2006; Orth et al. 2006; Waycott et al. 2009), where conservation efforts are challenged by a lack of maps, limited understanding of regional mechanisms driving ecosystem functioning, and limited public awareness of seagrass benefits (Orth et al. 2006; Unsworth et al. 2019a). The complex challenges of seagrass conservation require examination using multidisciplinary approaches. This multidisciplinary thesis examined processes and environmental conditions driving ecosystem functioning within and among eelgrass meadows and the provision of eelgrass ecosystem services in Atlantic Canada. **Chapter 2** created seasonal maps of three eelgrass meadows, contributing toward understanding eelgrass structural complexity and growth in Atlantic Canada. **Chapter 2** also exposed limitations and advantages associated with using a remotely piloted aircraft system (RPAS) to map submerged eelgrass in rapidly changing environments, in which I argued that increasing survey altitude could be worth the trade-off of acquiring lower resolution imagery to mitigate the risk of environmental conditions shifting mid-survey, a prominent issue when surveying submerged seagrass in temperate and boreal systems (Joyce et al. 2018; Nahirnick et al. 2019a). The subsequent two chapters examined the provision of two different ecosystem functions and services within and among three meadows, namely provision of fish habitat (**Chapter 3**) and coastal filtering nutrients into the surface sediment (**Chapter 4**). Both chapters provided evidence that eelgrass meadows support fish biodiversity and nutrient retention in the coastal zone, and that the provision of ecosystem services is meadow dependent. Eelgrass meadow structural complexity and the surrounding environment contribute to ecosystem functioning and ecosystem service outcome; however, traits driving ecosystem services may differ depending on the ecosystem service measured. In Placentia Bay, eelgrass presence, shallow water depth, and higher salinity were best attributed toward enhancing fish life history trait diversity in estuarine environments (**Chapter 3**). Salinity also best explained variability in C_{org} sources, and lower sediment bulk density enhanced nutrient retention in the surface sediment (**Chapter 4**). Finally, **Chapter 5** assessed societal recognition of eelgrass, which is necessary to obtain public support for seagrass conservation actions (Orth et al. 2006; Unsworth et al. 2019a). Contrary to general assessments of public perception of the ocean (Potts et al. 2016; Unsworth et al. 2019a; McKinley et al. 2020), this thesis shows that people residing in Canadian Atlantic coastal communities are familiar with eelgrass and their ecosystem services, exposing an opportunity to enhance eelgrass conservation efforts (**Chapter 5**). Such efforts could begin by refining current policies centered on protecting diverse eelgrass ecosystem services.

6.1 Addressing eelgrass conservation challenges

Challenge 1: Lack of seagrass maps

A deficiency of seagrass maps poses a significant limitation in understanding seagrass value and status, detecting early warnings of reduced seagrass resilience to threats such as climate change, and identifying local sources of threats (Unsworth et al. 2019a; Mckenzie et al. 2020). RPAS are increasingly popular tools in seagrass research as they enable georeferenced spatial data to be acquired at the meadow-scale, offering a different perspective of seagrass meadows compared to more conventional methods, such as snorkel or SCUBA surveys, and at a lower cost compared to other aerial survey methods, such as aerial surveys from an airplane (Joyce et al. 2018). **Chapter 2** shows that PRAS can be used to map the extent of submerged eelgrass meadows, and that challenges associated with surveying submerged eelgrass in rapidly changing environmental conditions can be overcome by flying higher with little detriment to the survey. However, findings in **Chapter 2** also conform with previous research showing that RPAS imagery using RGB sensors is vulnerable to spectral overlap between habitats, particularly at habitat boundaries, and must be accompanied by *in situ* validation (e.g., (O'Neill et al. 2011; Ventura et al. 2018; Tait et al. 2019). I show this to be especially necessary in temperate Atlantic Canada, as spectral signatures of different habitats, including seagrass, macroalgae, and deep water, are occasionally indistinguishable (**Chapter 2**). Remote sensing using multispectral sensors and alternative mapping classification approaches (e.g., object based image classification) could improve habitat mapping accuracy (Su et al. 2006; Tait et al. 2019; James et al. 2020), but are typically less accessible (e.g., more expensive, require higher computer power) and would still require validation. With eelgrass being wide-spread, acquiring validation data imposes a bottleneck in the speed at which reliable eelgrass maps can be acquired because resources necessary to collect validation data are limited, such as time and personnel in the field. Therefore, RPAS surveys may only be feasible to survey a subset of meadows within larger geographic scales (e.g., all Placentia Bay, across province, across country). Instead by accurately estimating eelgrass distribution (i.e., presence/absence), we can identify a representative subset of eelgrass meadows to map for monitoring of changes over time.

Accurate estimates of eelgrass distribution can be supplemented using citizen science. I showed substantial awareness of eelgrass by the public residing in coastal Atlantic Canada communities, as well as interest in having the public incorporated in eelgrass monitoring and conservation (**Chapter 5**). This suggests an opportunity to use the public to help meet mapping targets. Platforms enabling the public to share data on their local eelgrass meadows, pinpoint locations where eelgrass meadows have been observed, and upload imagery could serve as preliminary validation of eelgrass presence in remote sensing imagery (satellite and RPAS). This data could also be used to create a detailed map of eelgrass distribution range from which scientists and managers could use as a first step to identify where eelgrass meadows are. In fact, such platforms already exist (e.g., NETForce; SeagrassNet, www.seagrassnet.org; Seagrass Spotter, https://seagrassspotter.org/) but data uploads are few, limiting their utility for eelgrass mapping (Murphy et al. 2021). More effort promoting and applying data from these platforms could help accelerate the acquisition of reliable seagrass maps and improve seagrass monitoring.

Challenge 2: Understanding traits driving eelgrass ecosystem functions and services

The wide-spread distribution and heterogeneity of seagrass meadows requires decision-makers to select meadows of conservation priority (Unsworth et al. 2019a). Such management decisions would be aided with improved understanding of meadow traits that enhance the provision of ecosystem services. A trait-based framework could then be used to assist decision-makers evaluate trade-offs associated with prioritising one meadow over others (Suding et al. 2008; Unsworth et al. 2019a). By studying the provision of fish habitat and coastal filter function within the same three eelgrass meadows (**Chapters 3 and 4**), this thesis quantifies and compares the contribution of eelgrass meadow traits to the provision of different eelgrass ecosystem services. First, I provide evidence supporting the hypothesis that eelgrass meadows provide ecosystem services at different rates and extents (Boström et al. 2006; Nordlund et al. 2018a). Second, I identified habitat traits that enhanced two ecosystem services, namely fish habitat and nutrient retention. Although North Harbour maintained fish with more diverse life history traits (**Chapter 3**) and a high coastal filter function despite its smaller size (**Chapter 4**), I could not identify a common eelgrass meadow trait or set of traits underpinning these ecosystem services. Therefore, prioritizing ecosystem services for conservation focus may be necessary given that different components of ecosystem function are not supported by common traits.

The habitat traits underpinning nutrient retention in the three eelgrass meadows in Placentia Bay may be representative of traits that influence the role of eelgrass in the coastal filter at broader scales. The findings that sediment density relates to nutrient retention agrees with finding in other temperate regions, including studies conducted on the Canadian Pacific coast (Röhr et al. 2016, 2018; Postlethwaite et al. 2018; Prentice et al. 2020). However, the eelgrass meadows traits that have been found to enhance biodiversity are less consistent across geographic scales. Although studies have found that eelgrass presence often increases fish biodiversity, the specific aspects of eelgrass meadows (e.g., blade length, salinity) are less consistent (e.g., Santos et al. 2018; Wong and Kay 2019; Jones et al. 2021). This variability in traits driving biodiversity may be due to variability in the component species of communities, which vary regionally and seasonally (Cote et al. 2013). Therefore, my findings that depth and salinity were the significant traits driving biodiversity in eelgrass meadows may be primarily applicable to other eelgrass habitats in Placentia Bay and potentially other areas in Newfoundland. However, it is also important to note that functioning of eelgrass meadows extends beyond habitat boundaries, where surrounding environmental conditions and habitat connectivity contribute to eelgrass meadow functioning and ecosystem services (Nordlund et al. 2018a). Examination of these environmental traits was beyond the scope of this thesis. For example, exposure has been attributed to reduced nutrient retention in seagrass meadows (Röhr et al. 2016; Postlethwaite et al. 2018). Additionally, relative location to other coastal habitats such as kelp beds or relative location to anthropogenic infrastructure (e.g., aquaculture facilities) could alter species community composition (Cullain et al. 2018a; Murphy et al. 2019). Further research and management of seagrass meadows need to consider an ecosystem-based approach that encompasses the entire terrestrial and freshwater catchments as well as marine currents that flow into estuarine habitats (Unsworth et al. 2019a; Murphy et al. 2022).

Challenge 3: Limited public awareness

Raising public awareness of seagrass is an important first step toward reducing ill-informed decisions at individual and sector (e.g., government) levels that result in the degradation of seagrass meadows (Nordlund et al. 2018a; Unsworth et al. 2019a). Public awareness is also correlated to support for management actions. Generally, public awareness of seagrass is overshadowed by awareness for more charismatic coastal habitats such as coral reefs and mangroves (Duarte et al. 2008); however, such charismatic habitats do not occur in coastal Atlantic Canada. Instead, in this thesis I show that familiarity of eelgrass among the public residing in coastal Atlantic Canada (**Chapter 5**) is generally high. Despite this, Canadian legislation protecting eelgrass only focuses on the provision of fish habitat (Murphy et al. 2021), essentially disregarding other ecosystem services. This may be a consequence of limited eelgrass awareness among the general public, politicians, and decision-makers, whose access to coastal ecosystems may be more limited due to their location of residence (e.g., non-coastal) or a more urban lifestyle, resulting in eelgrass contribution to human well-being to be overlooked (Cullen-Unsworth et al. 2014; Lotze et al. 2018). Alternatively, this may be a consequence of the time it takes to translate science into policy.

6.2 Moving forward: Considerations for seagrass management and research

With the growing interest in seeking nature-based solutions for climate change mitigation and balancing the requirements of people and nature, there is increasing need to quantify the provision of ecosystem services and conserve systems supporting these services (Duarte et al. 2013; Unsworth et al. 2019a; Cooley et al. 2022). Despite this pressing need, seagrass research in Canada (and elsewhere; Nordlund et al. 2016; Ruiz-Frau et al. 2017) has been biased toward ecological services (e.g., fish and invertebrate habitat; **Chapter 5**). Only recently has research begun assessing social, cultural, and economic services, such as carbon sequestration and coastal protection (Ruiz-Frau et al. 2017). Consequently, the contribution of seagrass to societal wellbeing has likely been undervalued and inadvertently omitted during management decisions. For example, in Canadian policy, the only legislation protecting seagrass is the Fisheries Act, which focuses solely on the contribution of seagrass as a fish habitat (Murphy et al. 2021). Therefore, now that there is currently momentum behind seagrass research and identifying nature-based climate change solutions

(Cooley et al. 2022), the next step is to enhance public outreach, particularly in non-coastal areas, and for politicians to be aware of the full value and potential of seagrass ecosystems.

Implementation of new policies would contribute towards the mitigation of future seagrass meadow degradation. In addition to implementing policy that focuses on conservation of seagrass ecosystem services beyond fish habitat, policies could include consideration of the cumulative impacts of human activity on seagrass meadows, such as the combined effects of sediment deposition from coastal development and nutrient pollution from watershed land use (Murphy et al. 2021; 2022). Protection and restoration efforts would also assist seagrass recovery. However, the widespread decline of seagrass meadows over the past century (Waycott et al. 2009) requires areas for restoration and protection to be selected, as the immediate cost associated with such management measures is high. In this thesis, habitat traits driving both measured ecosystem services pointed towards the same eelgrass meadow (i.e., North Harbour) as the meadow to focus conservation efforts on. However, it is unlikely that a meadow will maximize the provision of all ecosystem services, which poses the question: how should we manage for different ecosystem services that are affected by different meadow traits? I suggest an early step in the decision-making process should include identifying priority ecosystem services relevant to the management region and target goals (e.g., seagrass as carbon sinks vs seagrass as food security; Fourqurean et al. 2012; Nordlund et al. 2016; Unsworth et al. 2019b), then identifying meadows containing the structural and environmental traits driving these services. Coincidently, continued research describing the heterogeneity within and among seagrass meadows and the resulting ecosystems services is necessary to better inform management decisions (Unsworth et al. 2019a). For instance, accounting for variability or region-specific contributions of seagrass meadows to carbon sequestration could result in more accurate valuation of seagrass contribution to offsetting carbon emissions. Valuation of carbon sequestering potential is important for knowing the consequences of losing seagrass meadows and for identifying where to prioritise conservation efforts when managing for nature-based climate change solutions. Mapping seagrass meadows and effective communication between researchers, the public, and managers prior to undertaking research can ensure that pertinent managerial questions are addressed, enable informed management decisions, and achieve public support behind management actions (Duarte et al. 2008; Unsworth et al. 2019a). This could be encouraged by matching research funding to questions surrounding conservation needs and to research promoting knowledge mobilization among sectors (Unsworth et al. 2019a).

6.3 Conclusion

This thesis examined the variability in ecosystem functioning and provision of ecosystem services among eelgrass meadows and related this heterogeneity to meadow structural complexity and surrounding environment. Although this thesis focuses on three eelgrass meadows in Placentia Bay, Newfoundland, findings from this thesis contribute to further overall understanding of seagrass ecosystem services across geographic regions. First, research in this thesis includes recommendations for conducting RPAS surveys in temperate regions and provides estimates of carbon storage in the surface sediment of eelgrass in a boreal system; a region that, to my knowledge, carbon storage in eelgrass meadows had yet to be measured. Additionally, this thesis contributes to the growing body of research examining the contribution of eelgrass meadows traits supporting biodiversity, which can assist with management planning (e.g., size of restoration patches) and monitoring (e.g., Warren et al. 2010; Cote et al. 2013; Wong and Dowd 2015; Murphy et al. 2019; Gagnon et al. 2023). The mapping recommendations in this thesis will assist researchers and other environmental working groups (e.g., NGOs, government) seeking to map seagrass meadows using RPAS and contributes to the improvement of regional and global seagrass distribution databases. By relating habitat traits to ecosystem services, findings from this thesis could assist local management decision-making while also contributing to global understanding of environmental and seagrass meadow structural traits that underpin the provision of ecosystem functions and resulting services. In doing so, these findings could contribute toward identifying a general framework for seagrass conservation in the future. Finally, whereas previous assessments have found public knowledge of seagrass to be limited globally (Unsworth et al. 2019a), this thesis exposes a strong relationship between research, government policies, and coastal community perception in Atlantic Canada; revealing an opportunity to expand on current conservation efforts. These efforts should begin by promoting knowledge mobilization of eelgrass with non-coastal communities enabling informed decision-making at the individual and organizational level, and by expanding conservation policies around protecting the full value of eelgrass meadows.

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Appendix A: Supporting information for Chapter 2

A1. Deploying GCPs and CPs

I placed markers for ground control points (GCPs) and check points (CPs) onshore surrounding the eelgrass meadows (see section *RPAS data processing* for application and see Supplementary Material for methods of deploying GCPs and CPs). Markers consisted of a rebar hammered into exposed substrate and georeferenced using three Trimble R10 Global Navigation Satellite System (GNSS) receivers (base, logging, and real-time kinematic (RTK) rover). The number of markers and their placement were limited by tree cover and substrate that was stable yet penetrable by the rebar (Table 2.1). Before each survey, I placed a $1m^2$ square plywood, painted in a black and white checkered pattern and with a hole in the middle over the rebar such that it protruded through the hole, enabling identification of the markers in the remotely piloted aircraft system (RPAS) images.

A2. Turbidity measurements

To assess whether water turbidity affected the quality of the RPAS data, a moored ECO-NTU turbidity sensor (Sea-Bird Scientific™, Washington, USA) was deployed in each site (Appendix A Figure S1). Each sensor was deployed as close to the eelgrass meadows as possible while ensuring the sensors remained over 1 m deep at low tide, which was required for them to function. Sensors were never more than 4 m deep at high tide as determined by the pressure sensor from a SeapHOx (Sea-Bird Scientific™, Washington, USA) moored with the turbidity sensors. The turbidity sensors were programed to record three measurements at 15 minute intervals from June-November 2020 for Swift Current and Baie de L’eau, and from August-November 2020 for North Harbour.

Table S2.1. Camera settings and image resolution for remotely piloted aircraft system (RPAS) surveys/images. ISO, shutter speed, and white balance were set prior to each survey while the RPAS hovered at flight altitude.

Site	Season	Flight altitude (m)	ISO	Shutter speed (sec.)	Image resolution (cm^2)
Swift Current	Summer	115	800	1/1600	10 × 10
	Fall		400	1/320	10 × 10
North Harbour	Summer	115	800	1/1600	10 × 10
	Fall		800	1/640.25	10 × 10
Baie de l'Eau	Summer	115	800	1/2000	10 × 10
	Fall		800	1/800	10 × 10
Capelin Cove	Summer	25	800	1/1600	10 × 10
		50	800	1/1600	10 × 10
		100	800	1/1600	10 × 10
Quadrat Altitude test	Summer	30.3	800	1/2000	0.46 × 0.46
		33.1	800	1/2000	0.50 × 0.50
		36.0	800	1/2000	0.54 × 0.54
		39.3	800	1/2000	0.59 × 0.59
		42.6	800	1/2000	0.64 × 0.64
		45.4	800	1/2000	0.69 × 0.69
		48.6	800	1/2000	0.74 × 0.74
		51.6	800	1/2000	0.78 × 0.78
		54.6	800	1/2000	0.83 × 0.83
		57.4	800	1/2000	0.87 × 0.87
		60.7	800	1/2000	0.92 × 0.92
		63.6	800	1/2000	0.96 × 0.96
		66.8	800	1/2000	1.01 × 1.01
		69.6	800	1/2000	1.05 × 1.05
		73.0	800	1/2000	1.11 × 1.11
		75.8	800	1/2000	1.15 × 1.15
		78.9	800	1/2000	1.19 × 1.19
		81.9	800	1/2000	1.24 × 1.24
		84.9	800	1/2000	1.29 × 1.29
		88.0	800	1/2000	1.33 × 1.33
		91.2	800	1/2000	1.38 × 1.38
		94.2	800	1/2000	1.43 × 1.43
		97.1	800	1/2000	1.47 × 1.47
		100.4	800	1/2000	1.52 × 1.52
		103.2	800	1/2000	1.56 × 1.56
		106.2	800	1/2000	1.61 × 1.61
		109.2	800	1/2000	1.65 × 1.65
		112.5	800	1/2000	1.70 × 1.70
		115.5	800	1/2000	1.75 × 1.75
		118.7	800	1/2000	1.80 × 1.80
		121.5	800	1/2000	1.84 × 1.84

Table S2.2. Count model coefficients for zero inflated poisson (ZIP) regression models relating macrolgae density estimates to season, site, and location. Two models were conducted for each survey method, remotely piloted aircraft system (RPAS) and snorkel transect survey. Models were generated using a log link.

		RPAS		
Covariate	Estimate (%)	Std. Error (%)	*P*-value	*95% CI*
Intercept	3.77	0.046	**<0.001**	[3.68, 3.86]
Summer	-0.52	0.042	**<0.001**	[-0.61, -0.44]
North Harbour	-0.36	0.050	**<0.001**	[-0.45, -0.23]
Swift Current	-0.40	0.056	**<0.001**	[-0.51, -0.29]
Inside	-0.17	0.055	**0.002**	[-0.27, -0.060]
Outside	0.17	0.050	**<0.001**	[0.068, 0.26]

		Snorkel		
Covariate	Estimate (%)	Std. Error (%)	*P*-value	*95% CI*
Intercept	2.57	0.063	**<0.001**	[2.46, 2.71]
Summer	-0.026	0.054	0.63	[-0.13, 0.079]
North Harbour	0.29	0.064	**<0.001**	[0.17, 0.42]
Swift Current	0.33	0.068	**<0.001**	[0.20, 0.47]
Inside	-0.82	0.11	**<0.001**	[-1.04, -0.61]
Outside	0.41	0.059	**<0.001**	[0.29, 0.52]

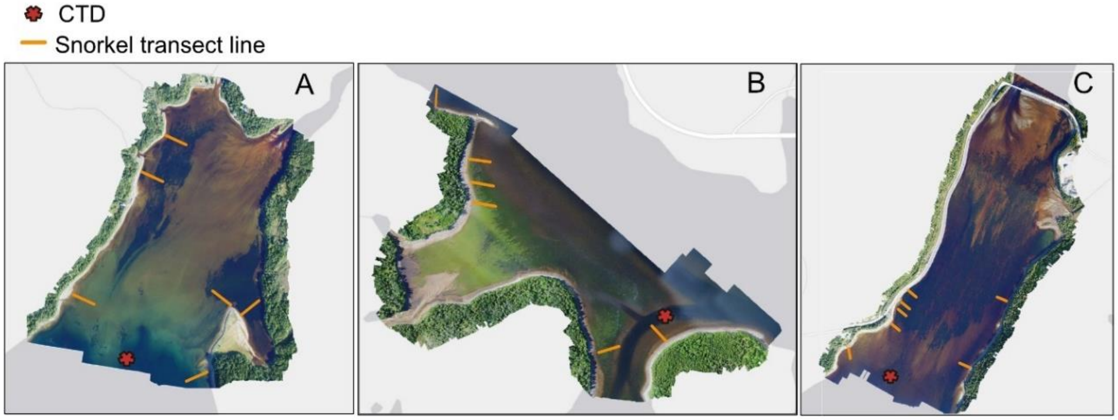

Figure S2.1. Schematic of snorkel transect (orange line) and turbidity sensor (red star) locations for A) North Harbour, B) Swift Current, and C) Baie de l'Eau. Light canvas grey base map was taken from Esri (2018) and projected from WGS 1984 to NAD1983 MTM zone 1 using ArcMap (v.10.7).

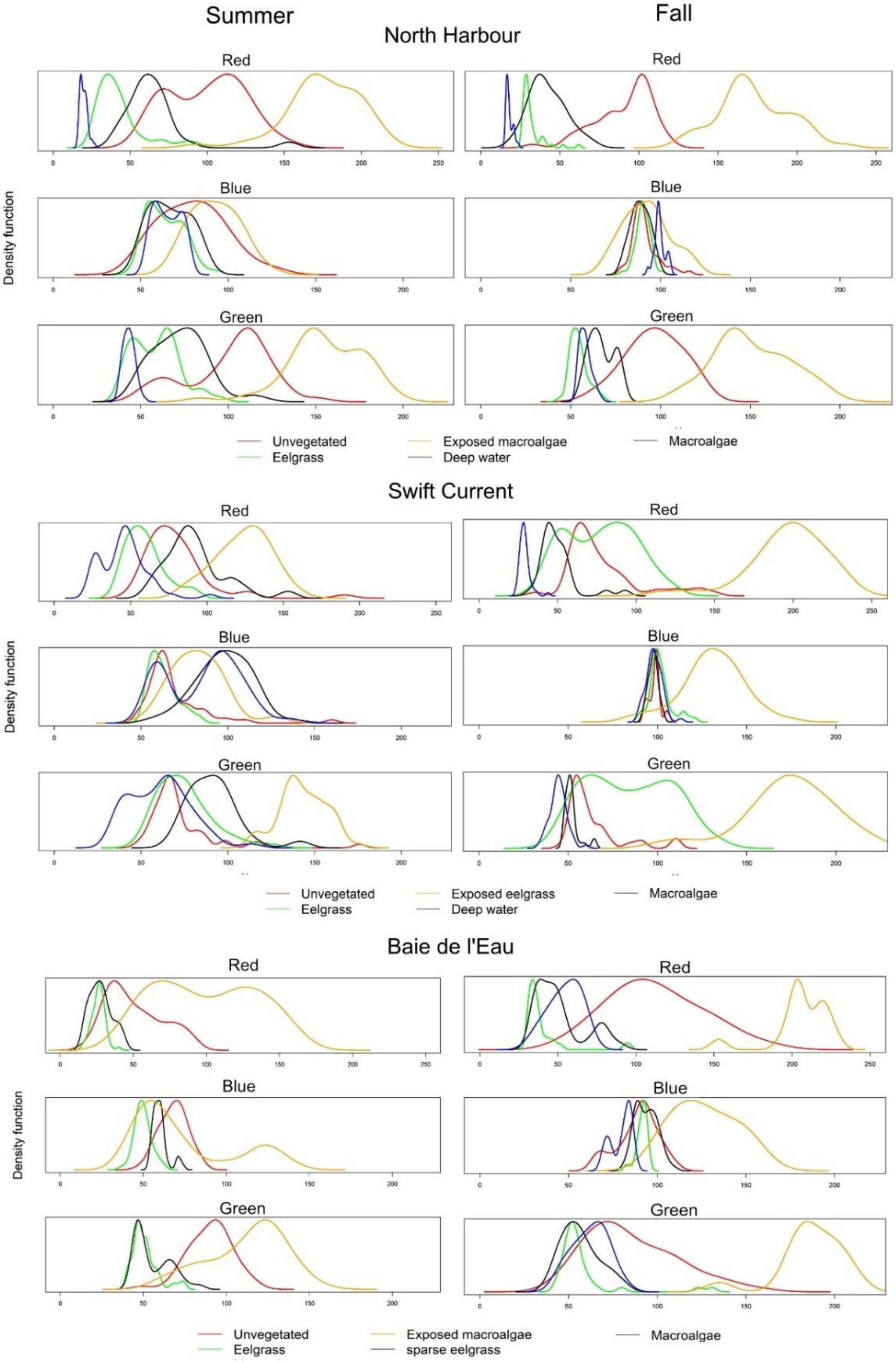

Figure S2.2. Kernel density curves of the pixel red, green blue colour composites for each class used to classify the remotely piloted aircraft system (RPAS) survey imagery.

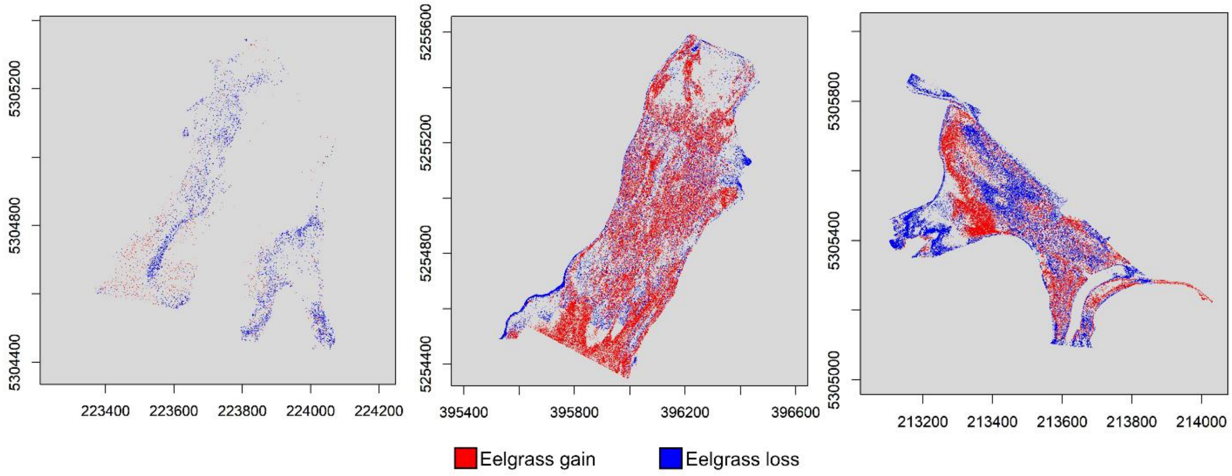

Figure S2.3. Differences in eelgrass cover between summer and fall surveys for A) North Harbour, B) Baie de l’Eau, and C) Swift Current. Blue represents pixels classified as eelgrass in the summer but not in the fall (i.e., eelgrass loss); red represents pixels that were classified as eelgrass in the fall but not the summer (i.e., eelgrass gain).

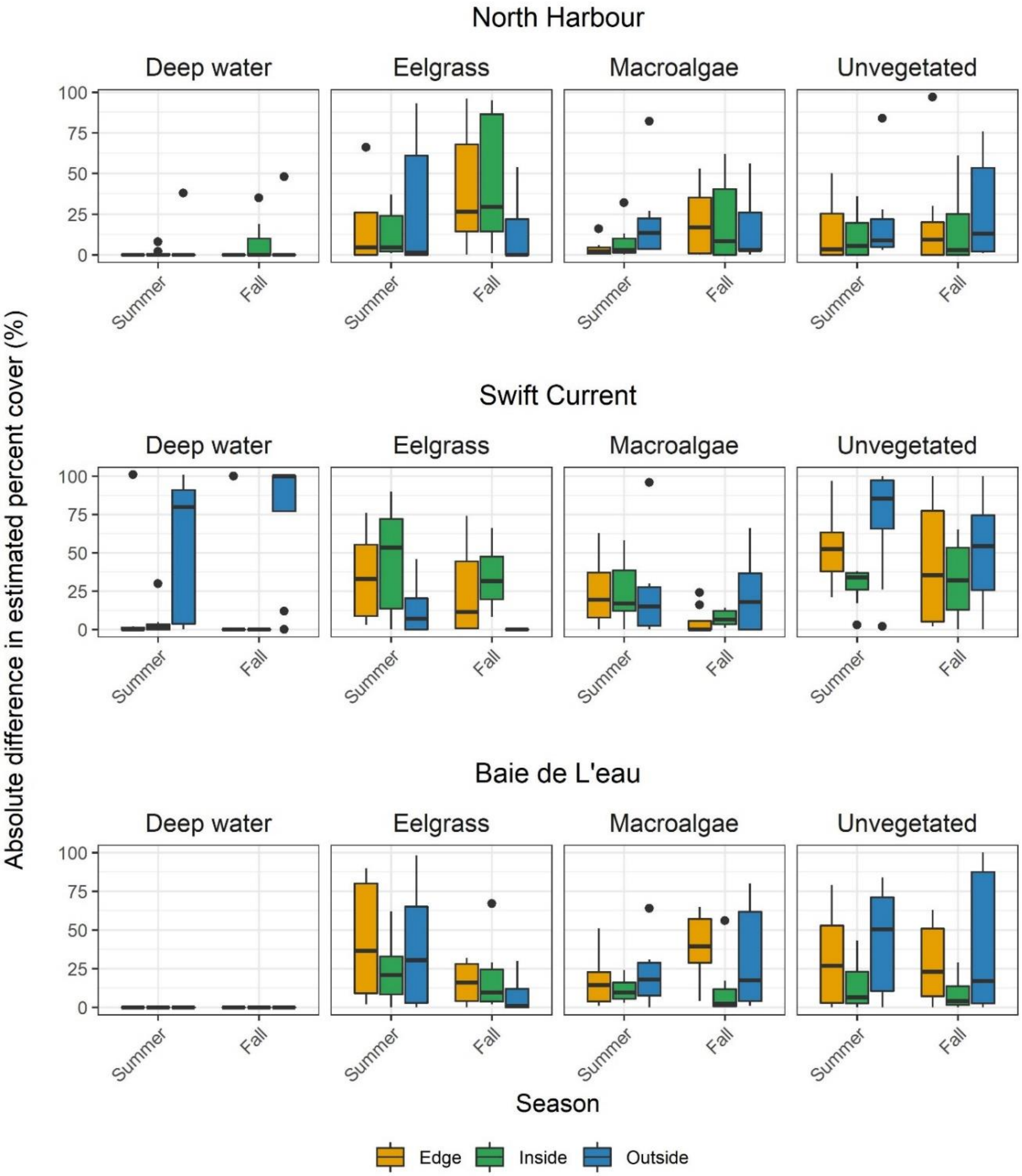

Figure S2.4. Boxplot of the differences (absolute values) in estimates of benthic composition (i.e., eelgrass, macroalgae, and unvegetated) cover between surveys using a remotely piloted aircraft system (RPAS) at 115 m altitude and snorkel quadrat surveys. Locations in the legend refer to the location of the quadrats relative to the eelgrass meadow.

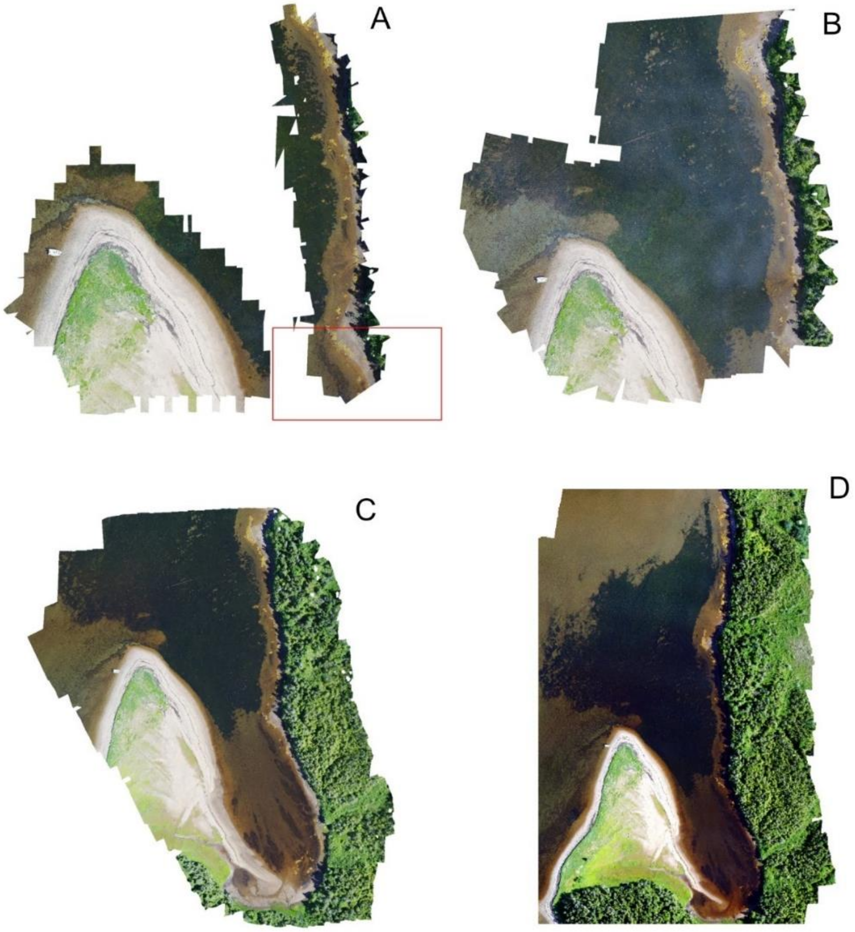

Figure S2.5. Orthomosaics of Caplin Cove at A) 25 m, B) 50m, C) 100 m, and D) 115 m. Red box delineates area where images aligned incorrectly.

Appendix B: Supporting information for Chapter 3

Table S3.1: Fish traits used to define life history trait diversity, where 1 signifies the species posses the trait and 0 signifies it does not.

Scientific name	**Common name**	**Size**			**Habitat in the water column**		
		Small	Medium	Large	Demersal	Benthopelagic	Pelagic
Pholis gunnellus	Rock gunnel	0	1	0	1	0	0
Gasterosteus aculeatus	Threespine stickleback	1	0	0	0	1	0
Gasterosteus wheatlandi	Blackspotted stickleback	1	0	0	0	1	0
Apeltes quadracus	Fourspine stickleback	1	0	0	0	1	0
Myoxocephalus scorpius	Shorthorn sculpin	0	1	0	1	0	0
Gadus ogac	Greenland cod	0	1	0	0	1	0
Pseudopleuronectes americanus	Winter flounder	0	1	0	1	0	0
Salmo salar	Atlantic salmon parr	0	1	0	0	1	0
Osmerus mordax	Rainbow smelt	0	0	1	0	0	1
Mallotus villosus	Capelin	1	0	0	0	0	1
Ammodytes americanus	Sand lance	0	0	1	0	1	0
Cyclopterus lumpus	Lumpfish	1	0	0	0	1	0
Urophycis tenuis	White hake	0	0	1	1	0	0
Gadus morhua	Atlantic cod	0	0	1	0	1	0
Clupea harengus	Atlantic herring	1	0	0	0	0	1
Caranx crysos	Blue runner	0	0	1	0	0	1
Salvelinus fontinalis	Brook trout	0	0	1	0	1	0
Salmo trutta	Brown trout	0	0	1	0	0	1
Tautogolabrus adspersus	Cunner	1	0	0	1	0	0
Myoxocephalus aenaeus	Grubby sculpin	0	1	0	1	0	0

Scientific name	Common name	Body shape					Behaviour
		Ribbon	Fusiform	Flat	Elongated	Compressiform	Schooling
Pholis gunnellus	Rock gunnel	1	0	0	0	0	0
Gasterosteus aculeatus	Threespine stickleback	0	1	0	0	0	1
Gasterosteus wheatlandi	Blackspotted stickleback	0	1	0	0	0	1
Apeltes quadracus	Fourspine stickleback	0	1	0	0	0	1
Myoxocephalus scorpius	Shorthorn sculpin	0	1	0	0	0	0
Gadus ogac	Greenland cod	0	1	0	0	0	0
Pseudopleuronectes americanus	Winter flounder	0	0	0	0	0	0
Salmo salar	Atlantic salmon parr	0	1	0	0	0	0
Osmerus mordax	Rainbow smelt	0	0	0	1	0	1
Mallotus villosus	Capelin	0	0	0	1	0	1
Ammodytes americanus	Sand lance	0	0	0	1	0	1
Cyclopterus lumpus	Lumpfish	0	0	0	0	1	0
Urophycis tenuis	White hake	0	1	0	0	0	0
Gadus morhua	Atlantic cod	0	1	0	0	0	0
Clupea harengus	Atlantic herring	0	1	0	0	0	1
Caranx crysos	Blue runner	0	1	0	0	0	1
Salvelinus fontinalis	Brook trout	0	1	0	0	0	0
Salmo trutta	Brown trout	0	1	0	0	0	0
Tautogolabrus adspersus	Cunner	0	1	0	0	0	0
Myoxocephalus aenaeus	Grubby sculpin	0	1	0	0	0	0
Myoxocephalus octodecemspinosus	Longhorn sculpin	0	1	0	0	0	0
Menidia menidia	Atlantic Silversides	0	0	0	1	0	1
Pleuronectes putnami	Smooth Flounder	0	0	1	0	0	0
Microgadus tomcod	Tomcod	0	1	0	0	0	0

Scientific name	**Common name**	**Reproduction behaviour**	**Use of eelgrass habitat**		
		Parental care	Coastal all life	Coastal refuge	Coastal foraging
Pholis gunnellus	Rock gunnel	1	1	0	0
Gasterosteus aculeatus	Threespine stickleback	1	1	0	0
Gasterosteus wheatlandi	Blackspotted stickleback	1	1	0	0
Apeltes quadracus	Fourspine stickleback	1	1	0	0
Myoxocephalus scorpius	Shorthorn sculpin	1	1	0	0
Gadus ogac	Greenland cod	0	1	0	0
Pseudopleuronectes americanus	Winter flounder	0	1	0	0
Salmo salar	Atlantic salmon parr	0	0	0	1
Osmerus mordax	Rainbow smelt	0	0	1	0
Mallotus villosus	Capelin	0	0	1	0
Ammodytes americanus	Sand lance	0	0	1	0
Cyclopterus lumpus	Lumpfish	1	0	1	0
Urophycis tenuis	White hake	0	0	1	0
Gadus morhua	Atlantic cod	0	0	1	0
Clupea harengus	Atlantic herring	0	0	0	1
Caranx crysos	Blue runner	0	0	1	0
Salvelinus fontinalis	Brook trout	0	0	0	1
Salmo trutta	Brown trout	0	0	0	1
Tautogolabrus adspersus	Cunner	0	1	0	0
Myoxocephalus aenaeus	Grubby sculpin	0	1	0	0
Myoxocephalus octodecemspinosus	Longhorn sculpin	0	1	0	0
Menidia menidia	Atlantic Silversides	0	1	0	0
Pleuronectes putnami	Smooth Flounder	0	1	0	0
Microgadus tomcod	Tomcod	0	0	1	0

Scientific name	**Common name**	**Migration**			**Egg type**	
		Resident	Anadromous	Ocean migrant	Eggs Demersal	Eggs Pelagic
Pholis gunnellus	Rock gunnel	1	0	0	1	0
Gasterosteus aculeatus	Threespine stickleback	1	0	0	1	0
Gasterosteus wheatlandi	Blackspotted stickleback	1	0	0	1	0
Apeltes quadracus	Fourspine stickleback	1	0	0	1	0
Myoxocephalus scorpius	Shorthorn sculpin	1	0	0	1	0
Gadus ogac	Greenland cod	1	0	0	1	0
Pseudopleuronectes americanus	Winter flounder	1	0	0	1	0
Salmo salar	Atlantic salmon parr	0	1	0	1	0
Osmerus mordax	Rainbow smelt	0	1	0	1	0
Mallotus villosus	Capelin	0	0	1	1	0
Ammodytes americanus	Sand lance	0	0	1	1	0
Cyclopterus lumpus	Lumpfish	0	0	1	1	0
Urophycis tenuis	White hake	0	0	1	0	1
Gadus morhua	Atlantic cod	0	0	1	0	1
Clupea harengus	Atlantic herring	0	0	1	1	0
Caranx crysos	Blue runner	0	0	1	0	1
Salvelinus fontinalis	Brook trout	0	1	0	1	0
Salmo trutta	Brown trout	0	1	0	1	0
Tautogolabrus adspersus	Cunner	1	0	0	0	1
Myoxocephalus aenaeus	Grubby sculpin	1	0	0	1	0
Myoxocephalus octodecemspinosus	Longhorn sculpin	1	0	0	1	0
Menidia menidia	Atlantic Silversides	1	0	0	1	0
Pleuronectes putnami	Smooth Flounder	1	0	0	1	0
Microgadus tomcod	Tomcod	0	0	1	1	0

Scientific name	Common name	Egg size		
		Egg small	Egg medium	Egg large
Pholis gunnellus	Rock gunnel	0	0	1
Gasterosteus aculeatus	Threespine stickleback	0	1	0
Gasterosteus wheatlandi	Blackspotted stickleback	0	1	0
Apeltes quadracus	Fourspine stickleback	0	1	0
Myoxocephalus scorpius	Shorthorn sculpin	0	0	1
Gadus ogac	Greenland cod	0	1	0
Pseudopleuronectes americanus	Winter flounder	1	0	0
Salmo salar	Atlantic salmon parr	0	0	1
Osmerus mordax	Rainbow smelt	1	0	0
Mallotus villosus	Capelin	1	0	0
Ammodytes americanus	Sand lance	1	0	0
Cyclopterus lumpus	Lumpfish	0	0	1
Urophycis tenuis	White hake	1	0	0
Gadus morhua	Atlantic cod	0	1	0
Clupea harengus	Atlantic herring	0	1	0
Caranx crysos	Blue runner	1	0	0
Salvelinus fontinalis	Brook trout	0	0	1
Salmo trutta	Brown trout	0	0	1
Tautogolabrus adspersus	Cunner	1	0	0
Myoxocephalus aenaeus	Grubby sculpin	0	1	0
Myoxocephalus octodecemspinosus	Longhorn sculpin	0	0	1
Menidia menidia	Atlantic Silversides	1	0	0
Pleuronectes putnami	Smooth Flounder	0	1	0
Microgadus tomcod	Tomcod	0	0	1

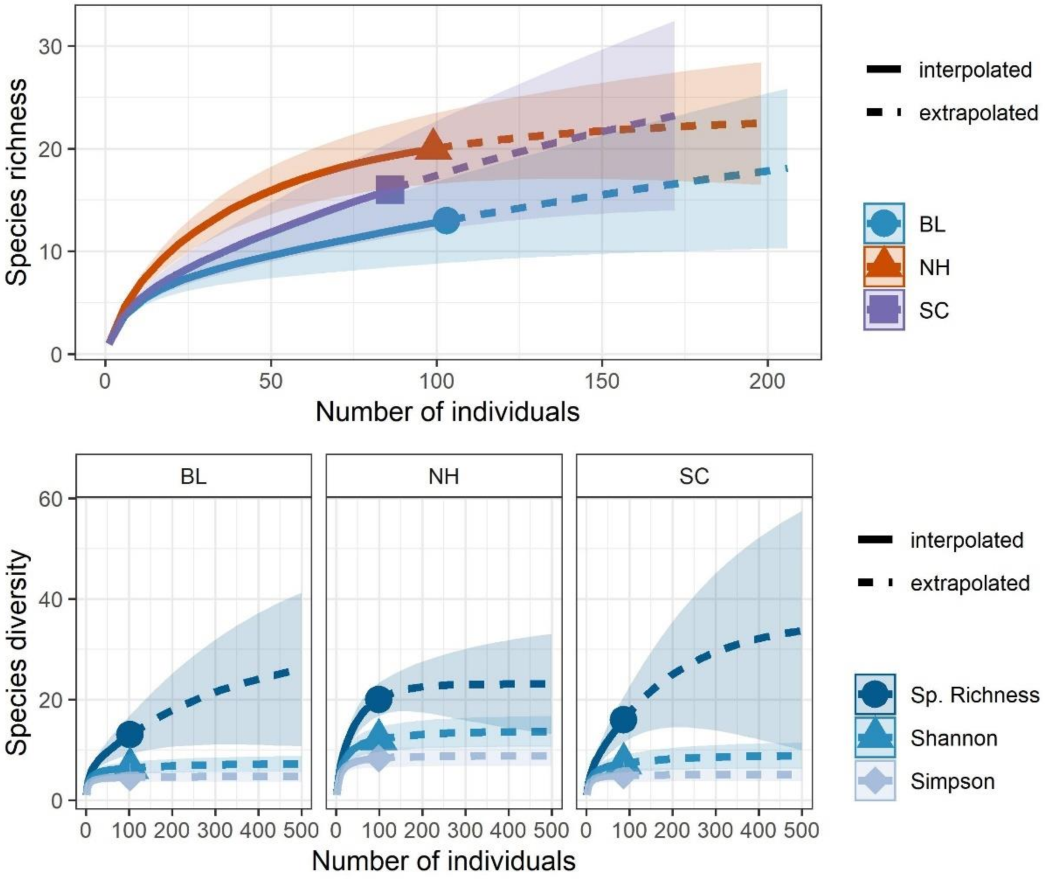

Figure S3.1: Species richness estimator (Chao1) showing how many more species may have been detected if the fish sampling period was extended in Baie de l'Eau (BL), North Harbour (NH) and Swift Current (SC). Fish were sampled using a seine net survey sampling 500 m^2 per tow. Figure was created using the iNext package (Hsieh et al. 2020; Chao et al. 2014) in R.

Appendix C: Supporting information for Chapter 4

C1. Equations for sediment variables

a) Degree of sorting

Calculated phi following methods outlined in Folk and Ward (1957)

b) Sediment bulk density

Bulk density = mass dry soil (g) ÷ volume of wet soil (mL)

c) C_{org} density (mg C_{org} cm^{-3})

C_{org} density = (%C_{org} ÷ 100) × Sediment bulk density × 1000

Where multiplying bulk density by 1000 converts it to mg/mL.

d) C_{org} stock (Mg C_{org} ha^{-1})

C_{org} stock = (C_{org} density × 5 cm) × (1 g ÷ 10^3 mg) × (1 Mg ÷ 10^6g) × ($10^8$$cm^2$ ÷ 1 ha)

Multiplying by 5 cm refers to the depth that sediment was sampled.

e) Particulate inorganic carbon (PIC)

%PIC = TOC - % C_{org}

Where TOC is the %C measured in the non-acidified sediment samples.

Table S4.1: Limit of detection (LOD), limit of quantitation (LOQ), and quality control (QC) sample error for the Costech ECS 4010/Thermo DELTA V Advantage IRMS used for sediment nutrient and isotope analyses.

Analysis	**LOD (µg)**	**LOQ (µg)**	**Error of Sample % Error**	**SD of Sample % Error**	**Error of Isotope Error (‰)**	**SD of Isotope Error (‰)**
Carbon	0.3	1.0	1.1	1.6	0.052	0.150
Nitrogen	0.7	1.9	2.0	2.5	0.123	0.263

Table S4.2: Regression models identifying covariates that best explain the variability in sediment carbon content. %C_{org} is a percentage bound between 0 and 1, therefore variability in %C_{org} was evaluates using a beta regression model with a logit link. A gamma distribution with a log link function was applied for evaluating variability in C_{org} density, and a Gaussian distribution was used for $\delta^{13}C_{org}$. All models had transect ID as a random effect to account for dependencies between samples. Correlated covariates were excluded from the full model, and the most parsimonious models were then identified using stepwise model selection according to lowest AIC scores. Statistically significant explanatory variables are highlighted in bold.

Dependent variable	Covariate	AIC	df	Estimate	SD	*Z*	p-value
C_{org} (%)	Null *(RE only)*	-282	49	-	-	-	-
	Sediment bulk density	-331		-1.68	0.17	-9.7	<**0.001**
	Eelgrass percent cover			0.0037	0.0019	1.9	0.060
C_{org} density (mg C_{org} cm^{-3})	Null *(RE only)*	416	47	-	-	-	-
	Temperature	421		-0.26	0.31	-0.86	0.39
	Salinity			-0.088	0.15	-0.58	0.56
	Sediment mud content			0.096	0.75	1.3	0.20
	Eelgrass percent cover			0.006	0.004	1.4	0.17
$\delta^{13}C_{\mathbf{org}}$ (‰)	Null *(RE only)*	164	46	-	-	-	-
	Temperature	164		-0.49	0.50	-0.98	0.33
	Salinity			-1.18	0.25	-4.7	<**0.001**
	Sediment bulk density			-0.059	0.12	1.1	0.64
	Sediment mud content			0.38	0.34	-0.5	0.27
	Eelgrass percent cover			0.0088	0.0072	1.2	0.22

Table S4.3: Regression models identifying covariates that best explain the variability in carbon data within the eelgrass meadow. Outside transects were excluded because eelgrass values of length and width zero would be misleading. %C_{org} is a percentage bound between 0 and 1, therefore variability in %C_{org} was evaluates using a beta regression model with a logit link. A gamma distribution with a log link function was applied for evaluating variability in C_{org} density, and a Gaussian distribution was used for $\delta^{13}C_{org}$. All models had transect ID as a random effect to account for dependencies between samples. Correlated covariates were excluded from the full model, and the most parsimonious models were then identified using stepwise model selection according to lowest AIC scores. Statistically significant explanatory variables are highlighted in bold.

Dependent variable	Covariate	AIC	df	Estimate	SD	*Z*	p-value
C_{org} (%)	Null *(RE only)*	-205	30	-	-	-	-
	Sediment bulk density	-207		-1.8	0.2	-9.0	**<0.001**
	Eelgrass percent cover			0.0046	0.0026	1.8	0.080
	Sediment mud content			-0.063	0.033	-1.9	0.054
C_{org} density (mg C_{org} cm^{-3})	Null *(RE only)*	281	32	-	-	-	-
	Temperature	276		0.28	0.23	1.2	0.22
$\delta^{13}C_{org}$ (‰)	Null *(RE only)*	119	27	-	-	-	-
	Temperature	119		-0.36	0.55	-0.6	0.52
	Salinity			-1.81	0.35	-5.2	**<0.001**
	Sediment bulk density			-0.21	0.13	0.93	0.10
	Sediment mud content			0.49	0.53	-1.6	0.35
	Eelgrass percent cover			0.044	0.016	2.9	**0.0043**
	Eelgrass blade length			-0.0031	0.0028	-1.1	0.27

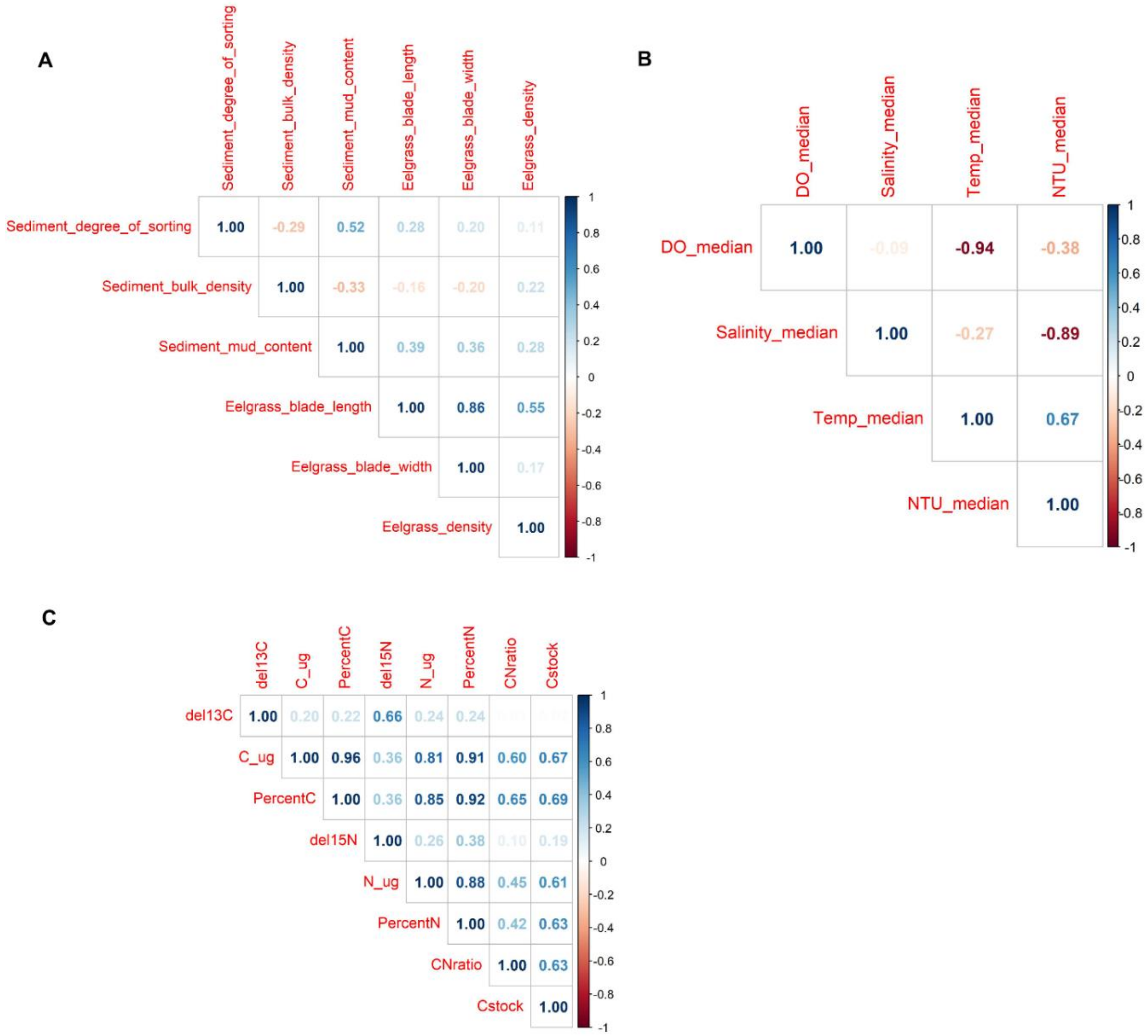

Figure S4.1: Correlation between covariates used to explain variability in C_{org}, C_{org} density, and $\delta^{13}C_{org}$ generalized linear models. Covariates with a $r < -0.6$ or $r > 0.6$ were deemed colinear.

Appendix D: Online questionnaire used to collect data for Chapter 5

PART 1 – OBSERVATIONS AND EXPERIENCES WITH EELGRASS MEADOWS

In this section, we would like to know your experiences and observations of how eelgrass meadows have changed over time. The following questions inquire about how eelgrass meadowshave changed over time and whether observed changes coincide with changes in animal (e.g. fish) abundance.

Please read the following description:

Eelgrass (*Zostera marina*) is a species of marine plant that often grow near estuaries and create vast underwater meadows in shallow marine coastal environments. Eelgrass consist of a networkof roots anchoring the plant below the sediment, and long, green vertical blades that protrude through the sediment into the water column.

Photo credit: Dr. Arnault Lebris

https://seagrassesinclasses.mdibl.org/wp-content/uploads/2012/01/eelgrass-reproduction-facts.pdf

http://intertidal-novascotia.blogspot.com/2012/05/zostera-marina-common-eelgrass.html

1. Have you observed any eelgrass within 50km from where you reside? If so, please enter the year/year range that you noticed the eelgrass in the blank provided (e.g., 1996-2007; 1996-2019).

☐ No, I have not noticed any eelgrass
☐ Yes, I have noticed eelgrass (please specify the years)

2. In your opinion, human activity generally has a positive effect on eelgrass meadows (please select one).

- ☐ Strongly agree
- ☐ Moderately agree
- ☐ Somewhat agree
- ☐ Neither agree nor disagree
- ☐ Somewhat disagree
- ☐ Moderately disagree
- ☐ Strongly disagree
- ☐ I do not know

3. In your opinion, human activity generally has a negative effect on eelgrass meadows (please select one).

- ☐ Strongly agree
- ☐ Moderately agree
- ☐ Somewhat agree
- ☐ Neither agree nor disagree
- ☐ Somewhat disagree
- ☐ Moderately disagree
- ☐ Strongly disagree
- ☐ I do not know

4. Since you began observing eelgrass:

i. The number of eelgrass meadows in the coastal areas you frequent have (please select one)

- ☐ Increased a lot
- ☐ Increased
- ☐ Did not change
- ☐ Decreased
- ☐ Decreased a lot
- ☐ I do not know

ii. The overall size of eelgrass meadows in the coastal areas you frequent have (please select one)

☐ Decreased
☐ Decreased a lot
☐ Did not change
☐ Increased a lot
☐ Increased
☐ I do not know

iii. The shoreline surrounding around eelgrass meadows has (please select one).

☐ Change a lot
☐ Changed somewhat
☐ Has not changed

iv. Local fish abundance in and around eelgrass meadows has (please select one).

☐ Increased a lot
☐ Increased
☐ Did not change
☐ Decreased
☐ Decreased a lot
☐ I do not know

v. The harbor infrastructure and/or activities around the eelgrass meadows you observe (e.g., addition of infrastructure such as marinas, wharves, aquaculture farms, dredging) (please select one).

☐ Has not changed
☐ Has decreased
☐ Has decreased a lot
☐ Has increased
☐ Has increased a lot
☐ I do not know

vi. The level of pollution in the water around these eelgrass meadows has (please select one).

☐ Increased a lot

☐ Increased
☐ Did not change
☐ Decreased
☐ Decreased a lot
☐ I do not know

5. In your opinion, what are the main causes of any changes in eelgrass meadows you have observed? (Please select all that apply)

☐ Agricultural runoff
☐ Climate change
☐ Coastal development
☐ Competition with other marine plant species
☐ Disease
☐ Household wastewater
☐ Municipal sewage
☐ Aquaculture
☐ Chemical dumping
☐ Invasive species
☐ Oil spill
☐ Predation
☐ Scouring
☐ I do not know
☐ None of these
☐ Other (please specify) ☐

6. Please specify, in your opinion, the top three causes for changes in eelgrass meadow coverage. Write N/A if there are no causes of change in eelgrass meadows.

☐ a. ☐
☐ b. ☐
☐ c. ☐

7. How have the change(s) in eelgrass meadows have affected you?

☐ Not at all
☐ Somewhat

☐ A lot
☐ I do not know
☐ There were no changes

8. In one or two sentences, please describe how the change(s) in eelgrass meadows have affected you, if they did.

PART 2 – VALUING EELGRASS MEADOWS

This section inquires about your observations and experience with the services that eelgrass meadows provide to you and the environment.

9. Ecosystem services are the benefits provided by an ecosystem that directly or indirectly contribute to human well-being. For instance, trees help clean the air you are breathing. After reading this definition, do you understand what ecosystem services are?

☐ Yes
☐ No
☐ Partially

10. In your opinion, do eelgrass meadows provide ecosystem services?

☐ Partially
☐ No
☐ Yes

11. Please rank, in your opinion, the top 5 ecosystem services provided by eelgrass, from (1) **most** important to (5) **least** important

☐ Appearance
☐ Animal habitat other than fish (e.g., birds)
☐ Climate change mitigation

☐ Coastal protection (i.e., current and wave regulation, sediment accretion, erosion stability)
☐ Compost fertilizer
☐ Mulch
☐ Cultural artefacts (e.g., spiritual and religious value)
☐ Education and research
☐ Fish habitat
☐ Food security (e.g., fish as food for humans or directly consuming eelgrass)
☐ Maintaining water quality (i.e., nutrient cycling, contamination regulation, oxygenation, carbon sequestration (capture and storage of carbon dioxide))
☐ Pharmaceuticals
☐ Raw material
☐ Recreation/tourism

12. Can you think of any other ecosystem services provided by eelgrass that were not included in the list? If not, write "no", if yes please list the other services.

13. In your opinion, eelgrass meadows are valuable.

☐ Strongly agree
☐ Agree
☐ Somewhat agree
☐ Neither agree nor disagree
☐ I do not know
☐ Disagree
☐ Somewhat disagree
☐ Strongly disagree

14. In your opinion, are other marine habitats more valuable than eelgrass? If yes, please provide up to three examples, if no, please write "no" and one sentence why.

15. In your opinion, do all eelgrass meadows in Atlantic Canada provide ecosystem services to the same degree?

☐ Yes
☐ Likely
☐ Unlikely
☐ No

16. Do you personally benefit from eelgrass meadows *directly*?

☐ Yes
☐ No

17. If you responded "Yes" in question 16, please list the services you gain from eelgrass ecosystems. If you responded "No", please write N/A in the comment box.

PART 3 – MANAGEMENT OF EELGRASS MEADOWS

This second last section inquires about your thoughts on the need to protect, restore and manage eelgrass meadows in areas you visit moving forward.

18. In your opinion, the following should pay for the protection and/or restoration of eelgrass meadows in Atlantic Canada (please select all that apply).

☐ Industry
☐ Government
☐ Communities
☐ Other (please specify)
☐ No one

19. In your opinion, we (Canadian North Atlantic societies) should do more to (please select all you agree with).

☐ Protect existing eelgrass meadows
☐ Restore eelgrass meadows

☐ No opinion
☐ There is no need to do more protection/restoration of eelgrass meadows

20. If you selected option “Protect existing eelgrass meadows” and/or “Restore eelgrass meadows” in question 19, what sort of management measures should we take to protect eelgrass meadows in Atlantic Canada? (Please select all that apply).

☐ Controlling the spreading of invasive species
☐ Establishing no boating areas
☐ Establishing no fishing areas
☐ Improving wastewater treatment
☐ Controlling development in coastal areas
☐ Mitigating the effects of climate change
☐ Other (please specify) ☐

21. In your opinion, eelgrass meadow restoration (please select all that apply)

☐ Should focus on meadows that have disappeared
☐ Should focus on meadows that are decreasing
☐ Should focus on meadows near communities
☐ Should focus on meadows far from communities, in remote coastal areas
☐ Is **not** an effective management measure
☐ I have no opinion
☐ I do not know what eelgrass meadow restoration involves

22. In your opinion, the *federal* government should invest more in protecting and/or restoring eelgrass meadows in Canada.

☐ Strongly agree
☐ Agree
☐ Somewhat agree
☐ Neither agree nor disagree
☐ I do not know
☐ Strongly disagree
☐ Disagree
☐ Somewhat disagree

23. In your opinion, the *provincial* government should invest more in protecting and/or restoring eelgrass meadows in Canada.

☐ Neither agree nor disagree
☐ I do not know
☐ Strongly disagree
☐ Disagree
☐ Somewhat disagree
☐ Somewhat agree
☐ Agree
☐ Strongly agree

24. In your opinion the public should be more involved in the management and protection/restoration of eelgrass meadows.

☐ Strongly agree
☐ Agree
☐ Somewhat agree
☐ Neither agree nor disagree
☐ I do not know
☐ Somewhat disagree
☐ Disagree
☐ Strongly disagree

25. If you think the public should be more involved, what roles could the public play? (please select all that apply).

☐ Contribute opinions during management planning process
☐ Participate in restoration activities
☐ Assist with monitoring (i.e., citizen science)
☐ Community-based regulation of human impacts on eelgrass meadows
☐ I do not think the public should be more involved
☐ I do not know

26. Is there anything you wish you knew more regarding eelgrass in Atlantic Canada?

PART 4 – PARTICIPANT’S BACKGROUND

We are now going to ask general questions about you. This section provides us with context for comparing responses.

27. How old are you?

☐ 19-29
☐ 30-39
☐ 40-49
☐ 50-59
☐ 60-69
☐ 70-79
☐ 80+

28. How long have you resided in a Canadian Atlantic province (Prince-Edward Island, Nova Scotia, New Brunswick, Newfoundland and Labrador)? (Please write your response)

☐ Years ☐

29. Using the drop-down menus below, please select the options that best describe where you currently reside/spend part of the year.

Province ☐

Region ☐

30. How close is your Atlantic home/cottage/cabin to the coast?

☐ Less than 1km from the coast
☐ Between 1km and 4.9km from the coast
☐ Between 5km and 29.9km from the coast
☐ Between 30km and 50 km from the coast
☐ More than 50km from the coast

31. Does your current or previous job involve:
i. Working with an environmental conservation focus

☐ Yes, 75-100% of my job is/was in environmental conservation
☐ Yes, 50-75% of my job is/was in environmental conservation
☐ Yes, 25-50% of my job is/was in environmental conservation
☐ Yes, 25% of my job is/was in environmental conservation
☐ No, my job does/did not involve environmental conservation

ii. Working outdoors, near coastal habitats

☐ Yes, 9-12 months of the year
☐ Yes, 6-9 months of the year
☐ Yes, 3-6 months of the year
☐ Yes, 1-3 months of the year
☐ No

iii. Working in environmental education

☐ Yes, 9-12 months of the year
☐ Yes, 6-9 months of the year
☐ Yes, 3-6 months of the year
☐ Yes, 1-3 months of the year
☐ No

32. Do you fish?

☐ Yes, commercially
☐ Yes, recreationally
☐ Yes, commercially and recreationally
☐ No, I do not fish

33. How do you spend time on the coast in Atlantic Canada? (Please select all that apply)

☐ Boating
☐ Fishing
☐ Swimming

☐ Beachcombing
☐ Seadoing
☐ Surfing
☐ Paddle boarding
☐ Kayaking
☐ Diving/snorkeling
☐ Walking
☐ Other
☐ I do not spend time on the coast in Atlantic Canada

34. If you selected “Other” in the previous question, please specify in the comment box below. If you did not select “Other” in the previous question, please write N/A in the comment box.

35. What year did you start spending time on the beach or at sea? (enter response in blank space).

36. During what season(s) do you spend time on the beach or at sea? (please select all applicable options).

☐ Spring
☐ Summer
☐ Fall
☐ Winter

37. How many weeks per year do you normally spend on the coast in Atlantic Canada?

☐ < 1 week
☐ 1-2 weeks
☐ 2-4 weeks
☐ > 4 weeks
☐ All year

38. Are there any other comments you would like to add about eelgrass meadows in Atlantic Canada? If so, please write your comment below.

PART 5 – SURVEY FEEDBACK

This last section aims to obtain your thoughts on this survey.

39. Did you appreciate the opportunity to take this survey and share your experiences and observations about eelgrass meadows?

- ☐ Yes, a lot
- ☐ Yes
- ☐ Yes, somewhat
- ☐ Indifferent
- ☐ Not really
- ☐ No, not at all

Appendix E: Search term and search results for the literature review in Chapter 5

A literature review was conducted in the Web of Science using the term eelgrass AND the ecosystem service AND the study area of interest. Only studies that were conducted in Canada and discussed eelgrass ecosystem services were selected.

A) List of search terms

1. Eelgrass terms

Eelgrass

Seagrass

Zostera marina

2. Ecosystem Services

Compost

Fertilizer

Fish habitat

Food

Invertebrate habitat

Nursery

Juvenile fish

Pharmaceuticals

Raw materials

Vertebrate habitat

Bird habitat

Carbon sequestration

Insulation

Coastal protection

Geomorphology

Sediment accretion

Sediment stabilization

Animal food

Mariculture

Food

Water purification

Water quality

Bequest

Cultural artifacts

Education

Research

Spiritual

Tourism

Pollution

Eutrophication

3. Region of study

Canada

Table S5: Papers extracted from the literature review in Chapter 5.

Query	**Primary Ecosystem Service**	**Secondary Ecosystem Service**	**Title**	**Citation**
Animal Food	Fish Habitat	Invertebrate Habitat	Regional-scale effects of eutrophication on ecosystem structure and services of seagrass beds	Schmidt *et al.*, 2017
Carbon Sequestration	Carbon Sequestration		Low blue carbon storage in eelgrass (*Zostera marina*) meadows on the Pacific Coast of Canada	Postlethwaite *et al.*, 2018
Carbon Sequestration	Carbon Sequestration		Reduced water motion enhances organic carbon stocks in temperate eelgrass meadows	Prentice *et al.*, 2019
Carbon Sequestration	Carbon Sequestration		A Synthesis of Blue Carbon Stocks, Sources, and Accumulation Rates in Eelgrass (*Zostera marina*) Meadows in the Northeast Pacific	Prentice *et al.*, 2020
Carbon Sequestration	Carbon Sequestration		Blue Carbon Storage Capacity of Temperate Eelgrass (*Zostera marina*) Meadows	Rohr *et al.*, 2018
Coastal Protection	Research		From coast to coast to coast: ecology and management of seagrass ecosystems across Canada	Murphy *et al.*, 2021
Compost	Invertebrate Habitat	Eutrophication	Indirect effects of predators control herbivore richness and abundance in a benthic eelgrass (*Zostera marina*) mesograzer community	Amundrud *et al.*, 2015
Compost	Fish Habitat		The Role of Submerged Aquatic Vegetation in Structuring the Nearshore Fish Community Within an Estuary of the Southern Gulf of St. Lawrence	Schein *et al.*, 2012
Education	Research		Long-Term Eelgrass Habitat Change and Associated Human Impacts on the West Coast of Canada	Nahirnick *et al.*, 2019a
Education	Invertebrate Habitat		Latitude, temperature, and habitat complexity predict predation pressure in eelgrass beds across the Northern Hemisphere	Reynolds *et al.*, 2017
Eutrophication	Eutrophication		Inorganic nitrogen has a dominant impact on estuarine eelgrass distribution in the Southern Gulf of St. Lawrence, Canada	van den Heuvel *et al.*, 2019
Fish Habitat	Fish Habitat	Invertebrate Habitat	Comparative analysis of different survey methods for monitoring fish assemblages in coastal habitats	Baker *et al.*, 2016

Fish Habitat	Fish Habitat	Invertebrate Habitat; Juvenile Fish	Seabed Habitat Determines Fish and Macroinvertebrate Community Associations in a Subarctic Marine Coastal Nursery	Dalley *et al.*, 2017
Fish Habitat	Fish Habitat		Dominance determines fish community biomass in a temperate seagrass ecosystem	Eger *et al.*, 2021
Fish Habitat	Juvenile Fish	Fish Habitat	Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*)	Gorman *et al.*, 2009
Fish Habitat	Juvenile Fish	Fish Habitat	Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*)	Gotceitas *et al.*, 1997
Fish Habitat	Fish Habitat		Anthropogenic disturbance homogenizes seagrass fish communities	Iacarella *et al.*, 2018
Fish Habitat	Fish Habitat	Invertebrate Habitat	Spatial distribution of fishes and decapods in eelgrass (*Zostera marina* L.) and sandy habitats of a New Brunswick estuary, eastern Canada	Joseph *et al.*, 2006
Fish Habitat	Juvenile Fish		Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod *Gadus* spp.	Laurel *et al.*, 2003a
Fish Habitat	Fish Habitat		Strategies for restoring and developing fish habitats in the Strait of Georgia Puget-Sound Inland Sea, Northeast Pacific-Ocean	Levings *et al.*, 1991
Fish Habitat	Fish Habitat	Invertebrate Habitat	Linking eelgrass decline and impacts on associated fish communities to European green crab *Carcinus maenas* invasion	Matheson *et al.*, 2016
Fish Habitat	Fish Habitat		Seasonal distribution, abundance, and life-history traits of greenland cod, *Gadus ogac*, at Wemindji, Eastern James Bay	Morin *et al.*, 1991
Fish Habitat	Fish Habitat		A human impact metric for coastal ecosystems with application to seagrass beds in Atlantic Canada	Murphy *et al.*, 2019
Fish Habitat	Juvenile Fish	Fish Habitat	Habitat dependant growth of three species of bottom settling fish in a coastal fjord	Renkawitz *et al.*, 2011
Fish Habitat	Fish Habitat		The persistence and stability of fish assemblages within eelgrass meadows (*Zostera marina*) on the Pacific coast of Canada	Robinson and Yakimishyn, 2013
Fish Habitat	Eutrophicantion	Fish Habitat; Invertebrate Habitat	Regional-Scale Differences in Eutrophication Effects on Eelgrass-Associated (*Zostera marina*) Macrofauna	Schmidt *et al.*, 2012

Fish Habitat	Invertebrate Habitat		Species-specific relationships of invertebrates to vegetation in a seagrass bed .1. correlational studies	Schneider and Mann, 1991a
Fish Habitat	Bird Habitat		Decline of Canada geese (Branta canadensis) and common goldeneye (Bucephala clangula) associated with a collapse of eelgrass (*Zostera marina*) in a Nova Scotia estuary	Seymour *et al.*, 2002
Fish Habitat	Invertebrate Habitat		Beyond a single patch: local and regional processes explain diversity patterns in a seagrass epifaunal metacommunity	Stark *et al.*, 2020
Fish Habitat	Juvenile Fish	Fish Habitat	Fractal measures of habitat structure: maximum densities of juvenile cod occur at intermediate eelgrass complexity	Thistle *et al.*, 2010
Fish Habitat	Nursery	Juvenile Fish	Increasing density of juvenile Atlantic (*Gadus morhua*) and Greenland cod (*G. ogac*) in association with spatial expansion and recovery of eelgrass (*Zostera marina*) in a coastal nursery habitat	Warren *et al.*, 2010
Fish Habitat	Fish Habitat		A Model Framework to Determine the Production Potential of Fish Derived from Coastal Habitats for Use in Habitat Restoration	Wong and Dowd, 2016
Food	Vertebrate Habitat	Invertebrate Habitat	Ecosystem features determine seagrass community response to sea otter foraging	Hessing-Lewis *et al.*, 2018
Food	Invertebrate Habitat	Fish Habitat	Species-specific relationships of invertebrates to vegetation in a seagrass bed .2. experiments on the importance of macrphyte shape, epiphyte cover and predation	Schneider and Mann, 1991b
Food	Invertebrate Habitat	Juvenile Fish	Roberts Bank: Ecological crucible of the Fraser River estuary	Sutherland *et al.*, 2013
Invertebrate Habitat	Fish Habitat	Juvenile Fish	Habitat use by juvenile salmon, other migratory fish, and resident fish species underscores the importance of estuarine habitat mosaics	Chalifour *et al.*, 2019
Invertebrate Habitat	Invertebrate Habitat		A Biophysical Model and Network Analysis of Invertebrate Community Dispersal Reveals Regional Patterns of Seagrass Habitat Connectivity	Cristiani *et al.*, 2021
Invertebrate Habitat	Invertebrate Habitat	Fish Habitat	Higher abundance and diversity in faunal assemblages with the invasion of Codium fragile ssp fragile in eelgrass meadows	Drouin *et al.*, 2011

Invertebrate Habitat	Invertebrate Habitat		A comparison of epifaunal invertebrate communities in native eelgrass *Zostera marina* and non-native Zostera japonica at Tsawwassen, BC	Knight *et al.*, 2015
Invertebrate Habitat	Invertebrate Habitat		Rapid recovery of fauna following simulated ice rafting in a Nova-Scotain seagrass bed	Schneider and Mann, 1991
Invertebrate Habitat	Invertebrate Habitat		Epifaunal diversity patterns within and among seagrass meadows suggest landscape-scale biodiversity processes	Whippo *et al.*, 2018
Invertebrate Habitat	Invertebrate Habitat		Secondary Production of Macrobenthic Communities in Seagrass (*Zostera marina*, Eelgrass) Beds and Bare Soft Sediments Across Differing Environmental Conditions in Atlantic Canada	Wong, 2018
Juvenile Fish	Juvenile Fish	Nursery	Decreased lipid storage in juvenile Atlantic cod (*Gadus morhua*) during settlement in cold-water eelgrass habitat	Copeman *et al.*, 2008
Juvenile Fish	Juvenile Fish	Fish Habitat	Nearshore settlement and localized populations of Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland	Grant and Brown, 1998
Juvenile Fish	Juvenile Fish	Fish Habitat	Eelgrass as Valuable Nearshore Foraging Habitat for Juvenile Pacific Salmon in the Early Marine Period	Kennedy *et al.*, 2018
Juvenile Fish	Juvenile Fish	Fish Habitat	Settlement and distribution of age-0 juvenile cod, *Gadus morhua* and G-ogac, following a large-scale habitat manipulation	Laurel *et al.*, 2003b
Juvenile Fish	Nursery	Juvenile Fish	Temporal variability in the environmental and geographic predictors of spatial-recruitment in nearshore rockfishes	Markel *et al.*, 2017
Mariculture	Mariculture	Invertebrate habitat	Spatial Variation of Macroinfaunal Communities Associated with *Zostera marina* Beds Across Three Biogeographic Regions in Atlantic Canada	Cullain *et al.*, 2018a
Nursery	Nursery		Nearshore seascape connectivity enhances seagrass meadow nursery function	Olson *et al.*, 2019
Research	Invertebrate Habitat		Distribution and diversity of tunicates utilizing eelgrass as substrate in the western North Atlantic between 39 degrees and 47 degrees north latitude (New Jersey to Newfoundland)	Carman *et al.*, 2016
Research	Invertebrate Habitat		Biogeographical patterns of tunicates utilizing eelgrass as substrate in the western North Atlantic between 39 degrees	Carmen *et al.*, 2019

			and 47 degrees north latitude (New Jersey to Newfoundland)	
Research	Invertebrate Habitat	Eutrophication	Multiple stressors and disturbance effects on eelgrass and epifaunal macroinvertebrate assemblage structure	Cimon *et al.*, 2021
Research	Water quality	Invertebrate Habitat	Potential impacts of finfish aquaculture on eelgrass (*Zostera marina*) beds and possible monitoring metrics for management: a case study in Atlantic Canada	Cullain *et al.*, 2019b
Research	Invertebrate Habitat		Biodiversity mediates top-down control in eelgrass ecosystems: a global comparative-experimental approach	Duffy *et al.*, 2015
Research	Vertebrate Habitat		Physical disturbance by recovering sea otter populations increases eelgrass genetic diversity	Foster *et al.*, 2021
Research	Eutrophication	Carbon Sequestration	Eelgrass Bed Structure, Leaf Nutrient, and Leaf Isotope Responses to Natural and Anthropogenic Gradients in Estuaries of the Southern Gulf of St. Lawrence, Canada	Hitchcock *et al.*, 2017
Research	Invertebrate Habitat	Fish Habitat	Habitat alteration by invasive European green crab (*Carcinus maenas*) causes eelgrass loss in British Columbia, Canada	Howard *et al.*, 2019
Research	Bird Habitat	Fish Habitat; Invertebrate Habitat	Top-down control by great blue herons Ardea herodias regulates seagrass-associated epifauna	Huang *et al.*, 2015
Research	Bird Habitat		Meta-Analysis of Reciprocal Linkages between Temperate Seagrasses and Waterfowl with Implications for Conservation	Kollars *et al.*, 2017
Research	Invertebrate Habitat		Nonnative Species in British Columbia Eelgrass Beds Spread via Shellfish Aquaculture and Stay for the Mild Climate	Mach *et al.*, 2017
Research	Research		Remote Sensing of Shallow Coastal Benthic Substrates: In situ Spectra and Mapping of Eelgrass (*Zostera marina*) in the Gulf Islands National Park Reserve of Canada	O'Neill *et al.*, 2011
Research	Research		North Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina* L.	Olsen *et al.*, 2004
Research	Carbon Sequestration	Sediment Stabilization	Sea ice increases benthic community heterogeneity in a seagrass landscape	Pascal *et al.*, 2020
Research	Fish Habitat		Habitat heterogeneity in eelgrass fish assemblage diversity and turnover	Robinson *et al.*, 2011

Research	Research		Host-Specificity and Core Taxa of Seagrass Leaf Microbiome Identified Across Tissue Age and Geographical Regions	Sanders-Smith *et al.*, 2020
Research	Carbon Sequestration	Eutrophication	Ecosystem structure and services in eelgrass *Zostera marina* and rockweed Ascophyllum nodosum habitats	Schmidt *et al.*, 2011
Research	Carbon Sequestration	Coastal Protection	Microeukaryotic Communities Associated With the Seagrass *Zostera marina* Are Spatially Structured	Segovia *et al.*, 2021
Research	Juvenile Fish	Fish Habitat	Estuary habitat associations for juvenile Pacific salmon and pelagic fish: Implications for coastal planning processes	Sharpe *et al.*, 2019
Research	Fish Habitat	Fishery	The Effect of Region, Body Size, and Sample Size on the Weight-Length Relationships of Small-bodied Fishes Found in Eelgrass Meadows	Siegle *et al.*, 2014
Research	Mariculture	Water Quality	Reductions in distribution, photosynthesis, and productivity of eelgrass *Zostera marina* associated with oyster Crassostrea virginica aquaculture	Skinner *et al.*, 2013
Research	Mariculture	Eutrophication	Experimental determination of the effects of light limitation from suspended bag oyster (Crassostrea virginica) aquaculture on the structure and photosynthesis of eelgrass (*Zostera marina*)	Skinner *et al.*, 2014
Research	Invertebrate Habitat	Eutrophication	Bay-scale assessment of eelgrass beds using side scan and video	Vandermeulen, 2014
Research	Bird Habitat		North American Brant: effects of changes in habitat and climate on population dynamics	Ward *et al.*, 2005
Research	Invertebrate Habitat		Impact of predation-disturbance by large epifauna on sediment-dwelling harpacticoid copepods - field experiments in a subtidal seagrass bed	Webb and Parsons, 1991
Research	Fish Habitat		Climate change projections reveal range shifts of eelgrass *Zostera marina* in the Northwest Atlantic	Wilson and Lotze, 2019
Research			Branching Algorithm to Identify Bottom Habitat in the Optically Complex Coastal Waters of Atlantic Canada Using Sentinel-2 Satellite Imagery	Wilson *et al.*, 2020
Research	Invertebrate Habitat		Effects of invasive colonial tunicates and a native sponge on the growth, survival, and light attenuation of eelgrass (*Zostera marina*)	Wong and Vercaemer, 2012

Vertebrate Habitat	Fish Habitat	Invertebrate Habitat	Intertidal community structure differs significantly between substrates dominated by native eelgrass (*Zostera marina* L.) and adjacent to the introduced oyster Crassostrea gigas (Thunberg) in British Columbia, Canada	Kelly *et al.*, 2017
Water Quality	Water Quality		Photoacclimation and Light Thresholds for Cold Temperate Seagrasses	Leger-Daigle *et al.*, 2022
Water Quality	Carbon Sequestration	Fish Habitat	Large-Scale Differences in Community Structure and Ecosystem Services of Eelgrass (*Zostera marina*) Beds Across Three Regions in Eastern Canada	Namba *et al.*, 2018

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Appendix F: Supplemental figures for Chapter 5

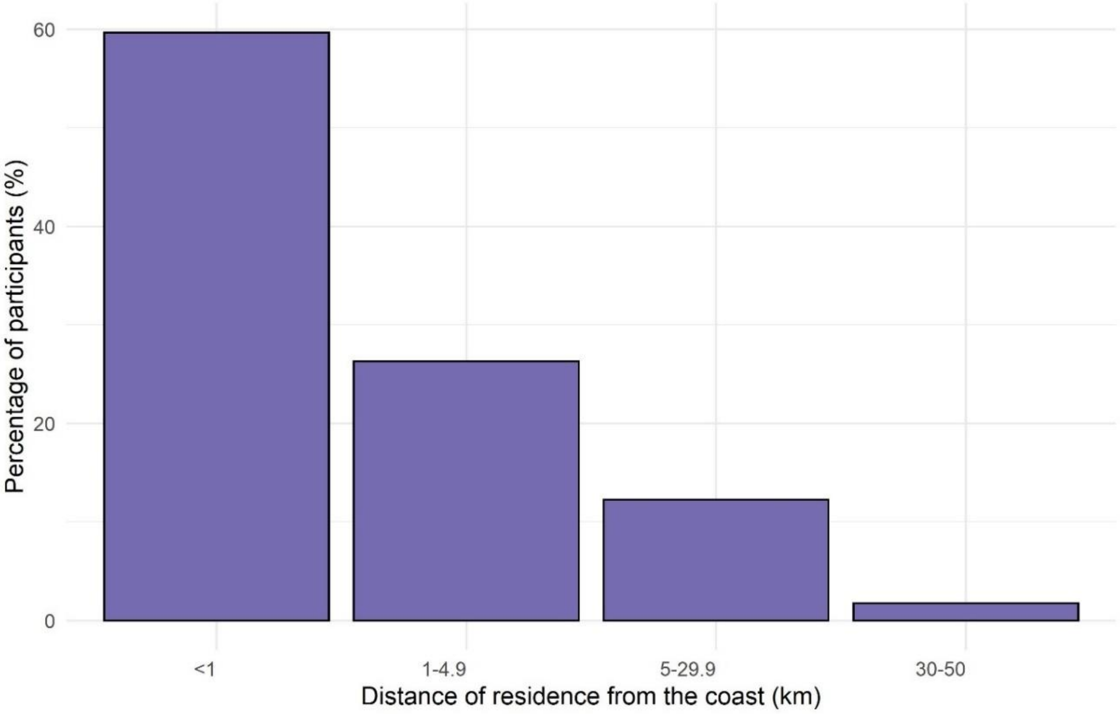

Figure S5.1: Distance of participants' residences from the coast (n=114).

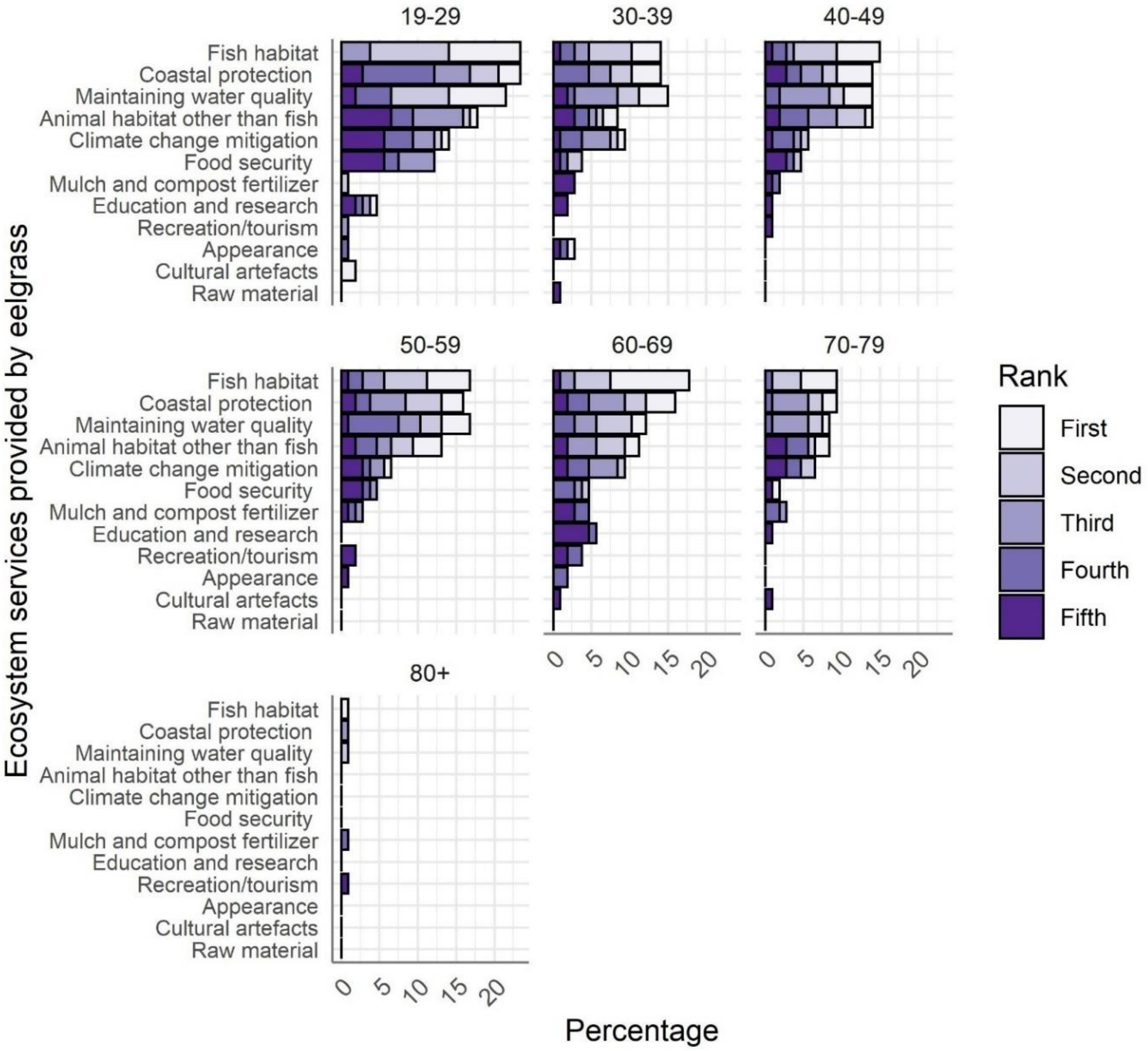

Figure S5.2: Participant ranking of eelgrass ecosystem services according to different age groups surveyed. Percent represents the proportion of individuals out of the total number of participants in each age class.

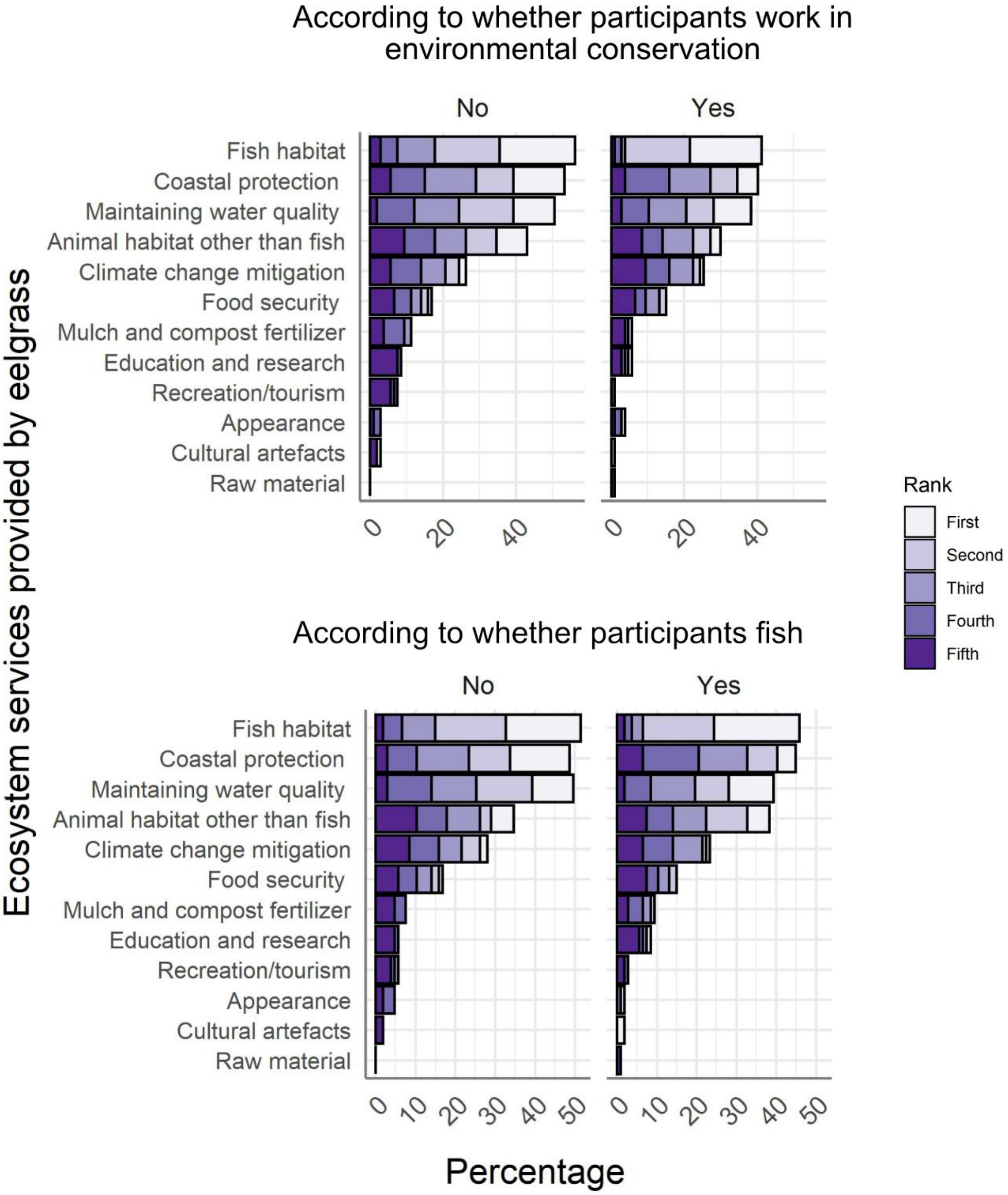

Figure S5.3: Participant ranking of eelgrass ecosystem services according to whether participants work in environmental conservation or fish. Percent represents the proportion of individuals out of the total number of participants that worked in environmental conservation or fished.

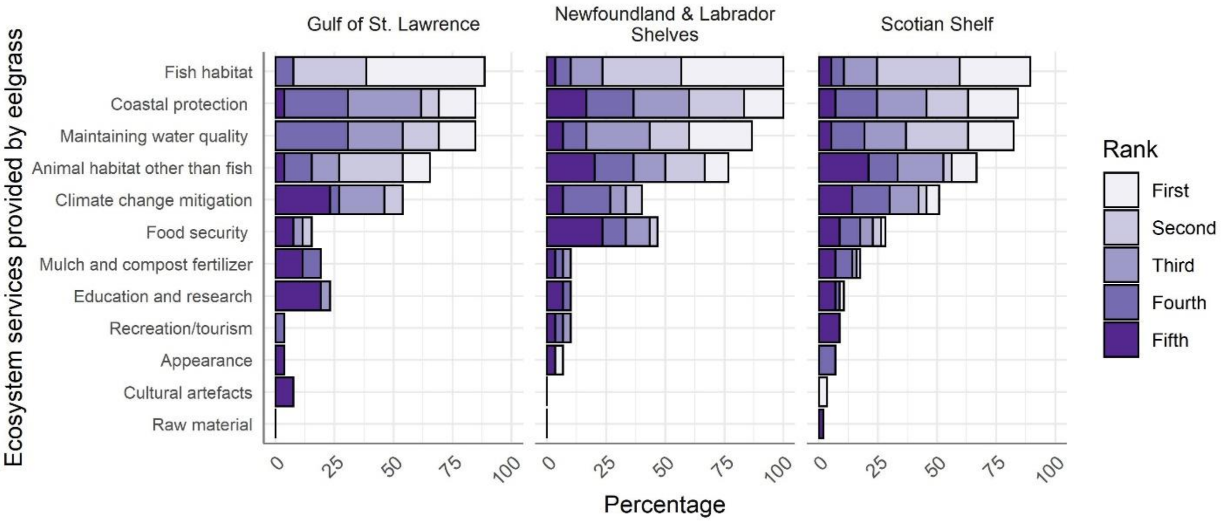

Figure S5.4: Participant ranking of eelgrass ecosystem services according to participants resident bioregion. Percent represents the proportion of individuals out of the total number of participants residing in each bioregion.

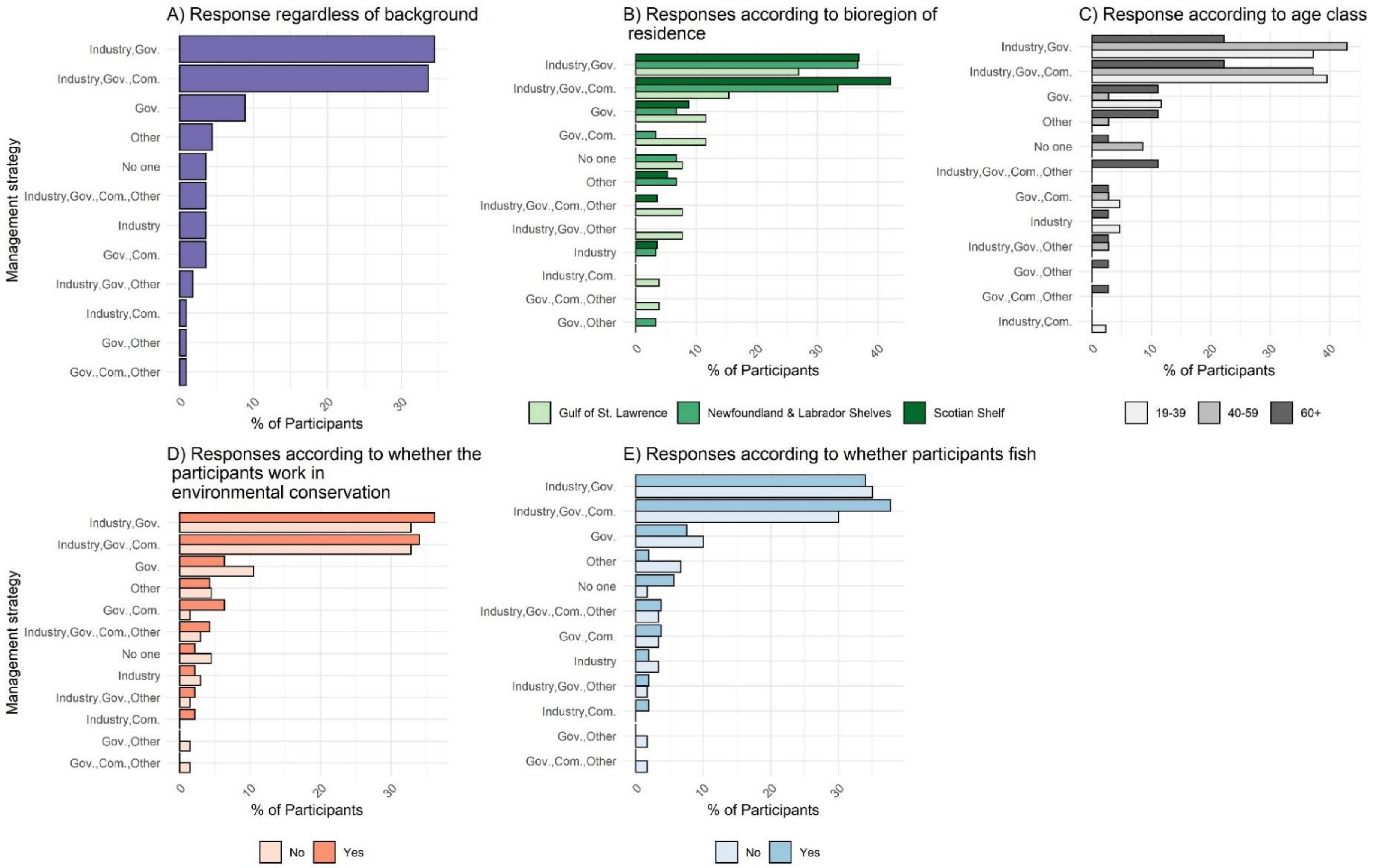

Figure S5.5: Groups (industry, government (Gov.), communities (Com.), or other) that should pay for eelgrass protection and restoration according to survey participants (n=114, except panel B where n=113).

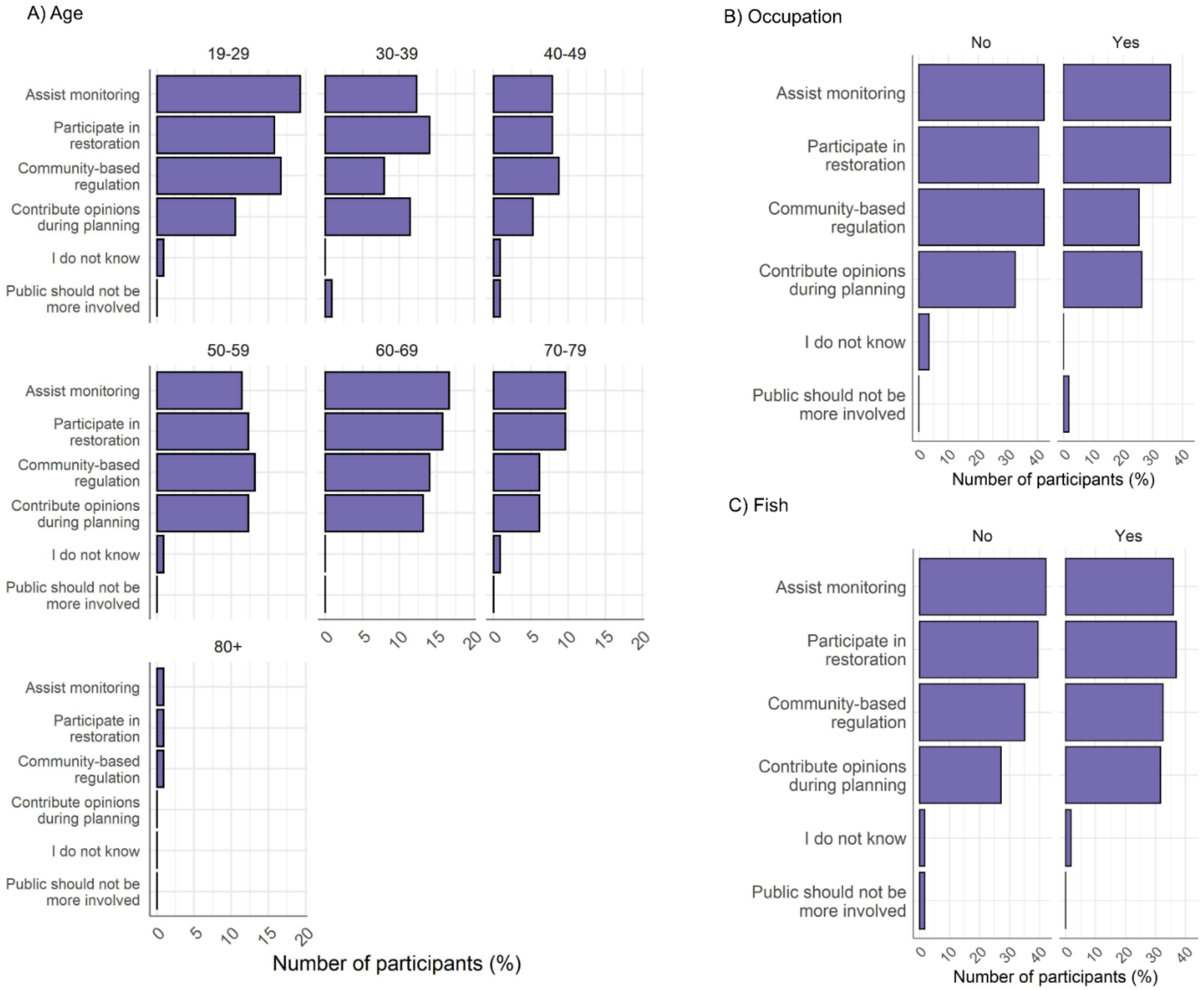

Figure S5.6: Public perception of ways that the public should be more involved in eelgrass management according to participant age, whether participants work in environmental conservation, or whether participants fish.